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THE FOSSIL ANTS OF NORTH AMERICA

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WITH ELEVEN PLATES.

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No. 1.— *The Fossil Ants of North America*¹

BY F. M. CARPENTER

I. INTRODUCTION

SIXTY-THREE years ago, when the first fossil insects were discovered in American Tertiary rocks, a new era began in the study of the geological history of the insects. Early expeditions under the stimulating leadership of Dr. S. H. Scudder, with the coöperation of the United States Geological Surveys, secured collections of over 20,000 specimens in the Florissant shales alone. For the most part, the material gathered at this time was described by Scudder between the years 1867 and 1900, when he was finally forced into inactivity by paralysis. For a short period of five years the Tertiary insects of the country were entirely neglected, but in 1905 the work was again taken up by the University of Colorado. The following year Professor W. M. Wheeler, Professor and Mrs. T. D. A. Cockerell, and S. A. Rohwer collected extensively at the Florissant locality, and in 1907 also a large expedition was made to the same beds under the direction of the American Museum of Natural History, Yale University, the University of Colorado, the British Museum of Natural History, and the Royal Irish Dublin Museum. The insects found on these two expeditions have chiefly been described by Professor Cockerell, Professor H. F. Wickham (Coleoptera), Professor C. T. Brues (Parasitic Hymenoptera), and S. A. Rohwer (Tenthredinoidea).

The long illness which Scudder endured after 1900, and which finally caused his death ten years later, prevented him from completing the investigations on the Florissant insects, so that when his collection was donated to the Museum of Comparative Zoölogy in 1902, fully half of the specimens were unstudied. This unworked material was found by Professor Wheeler to include over 4,000 ants which, together with as many more obtained on the later expeditions, were turned over to him for study. At about that time Professor Wheeler was occupied with the preparation of a monograph of the ants of the Baltic amber and after he had finished this task, he was prevented by other matters from carrying out his intention of describing the Florissant ant fauna. In 1925, at the suggestion of Dr. Wheeler, I undertook the study of these

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fossils, and have since been able to increase the collection to about 12,000 specimens, and to include ants from other American insect deposits. Some of this additional material was collected by the writer at Florissant, Colorado, and Green River, Wyoming, during the summer of 1927, but for the most part it has been received from the following sources: the United States National Museum, Washington, D. C.; Princeton University, Princeton, N. J.; the Carnegie Museum, Pittsburgh, Pa.; the Museum of Comparative Zoölogy, Cambridge, Mass.; Professor T. D. A. Cockerell, University of Colorado, Boulder, Colorado; Professor H. F. Wickham, University of Iowa, Iowa City, Iowa; Mr. Earl Douglass, Salt Lake City, Utah; and Professor J. H. Johnson, Colorado School of Mines, Golden, Colorado. To these contributors, as well as those mentioned before, I am greatly indebted for the use of their material.

For the privilege of examining and photographing the types of previously described fossil ants, I am especially indebted to Dr. E. M. Kindle, Canadian Geological Survey, Ottawa, Canada; Professor T. D. A. Cockerell, University of Colorado, Boulder, Colorado; Dr. R. S. Bassler, United States National Museum, Washington, D. C.; and Professor Nathan Banks, Museum of Comparative Zoölogy, Cambridge, Mass.

In designating the holotypes of the new species an attempt has been made to select the individuals showing most of the necessary characters, and since the Scudder collection includes much better material than the others, the majority of the holotypes are in the Museum of Comparative Zoölogy. Only one of the specimens secured on the 1907 expedition of the several museums mentioned above has been selected as a holotype, and at the suggestion of Professor Cockerell, who was in charge of the expedition, this has been placed in the same institution in order to keep as many of the holotypes together as possible. Professor Wickham has kindly donated the holotypes in his collection to the Museum of Comparative Zoölogy. Paratypes of the Florissant species have been allotted to the contributing institutions, so that the museums and universities listed above have as nearly a complete series of these ants as the number of duplicates has allowed.

To Professor W. M. Wheeler I am more than grateful for the suggestion of an investigation which has proved so interesting; for the use of his splendid collection of recent ants; and above all for the generous amount of time which he has spent with me discussing the fossils and their affinities. Indeed, without Professor Wheeler's assistance this task would never have been satisfactorily completed. Professor Brues

has also made many helpful suggestions and I am especially appreciative of his interest and encouragement, which has attended the work throughout.

Very little study has previously been made on the fossil ants of American deposits. Scudder described (1877a, 1878) four supposed ants from the Green River formation, and five others (1877b) from the Quesnel beds in British Columbia. Cockerell, more recently (1906, 1927), has described three species from Florissant, two from the Green River shales (1921, 1923b), and one from a small deposit in Brazos County, Texas (1923a). Professor Wheeler has briefly referred to these fossils in his general works on ants (1910, 1926, 1928), and in his study of the mountain ants of western North America (1917) has listed the genera of Florissant which he recognized by a cursory examination of the material at his disposal.

As a result of this neglect of the American forms, our knowledge of the geological history of the ants has been based almost exclusively upon the fossils found in the Tertiary formations of Europe, of which the most important is the Baltic amber (Oligocene). The ants contained in this resin belong to ninety-two species, referred by Mayr (1867) and Wheeler (1914) to the following genera: *Prionomyrmex*,* *Bradoponera*,* *Ectatomma*, *Electroponera*,* *Platythyrea*, *Euponera*, *Ponera*, *Sima*, *Monomorium*, *Erebomyrma*, *Vollenhovia*, *Stenamamma*, *Aphaenogaster*, *Electromyrmex** *Agroecomyrmex*,* *Myrmica*, *Nothomyrmica*,* *Leptothorax*, *Stiphomyrmex*,* *Enneamerus*,* *Protaneuretus*,* *Paraneuretus*,* *Dolichoderus*, *Iridomyrmex*, *Liometopum*, *Asymphylomyrmex*,* *Pityomyrmex*,* *Plagiolepis*, *Rhopalomyrmex*,* *Dimorphomyrmex*,¹ *Gesomyrmex*, *Prodimorphomyrmex*,* *Oecophylla*, *Prenolepis*, *Lasius*, *Formica*, *Glaphyromyrmex*,* *Pseudolasius*, *Dryomyrmex*,* and *Camponotus*. The Formicidae of the much rarer Sicilian amber were studied by Professor Carlo Emery (1891, 1913), who recognized the following genera: *Ectatomma*, *Ponera* (?), *Cataulacus*, *Hypomyrmex*,* *Podomyrmex*,* *Aëromyrma*, *Meranoplus*, *Leptothorax*, *Tapinoma*, *Technomyrmex*, *Plagiolepis*, *Gesomyrmex*, and *Oecophylla*. The two most productive of the Tertiary rock deposits of Europe, as far as insects are concerned, are at Radoboj in Croatia, and Oeningen in Baden. The ants of the Radoboj formation were described by Heer before our present conception of the genera of ants had been reached, so that the species were lumped into *Formica*, *Myrmica*, *Ponera*, and *Attopsis*. Fortunately, Mayr was able to examine a number of speci-

* Extinct.

¹ Recently shown by Wheeler to be synonymous with *Gesomyrmex* (Psyche, 36, p. 1-12, 1929).

mens determined by Heer, and to correct the generic determinations (1867). He considered that the following genera were represented: *Tetramorium* (?), *Prenolepis* (?), *Aphaenogaster*, *Myrmica* (?), *Cataulacus*, *Leptothorax* (?), *Dolichoderus*, *Liometopum*, *Lonchomyrmex*,* *Plagiolepis*, *Oecophylla*, *Lasius*, *Formica*, and *Camponotus*. The Oeningen ants were described by Heer also, at the same time, but since no myrmecologist has revised his determinations, we are obliged to disregard these ants at present.

Two deposits in the British Isles have yielded a few members of this family. From the older of these, the Bagshot beds of Bournemouth (Eocene), Cockerell has described (1920) two species, but since only the wings are preserved, the generic determinations are very dubious. The second deposit is at Gurnet Bay, Isle of Wight, and belongs to the Oligocene period. A few ants from there were first described by Cockerell (1915), and these were later revised and added to by H. St. J. K. Donisthorpe, the well-known British myrmecologist, who was able to examine a large series of these fossils (1920). The genera recognized by Donisthorpe include *Syntaphus*,* *Euponera*, *Ponera*, *Emplastus*,* *Dolichoderus*, *Leucotaphus*,* *Oecophylla*, and *Camponotus*. The ants of the other European deposits have not been sufficiently well treated to warrant their mention in this paper.

The study of fossil insects, with the exception of most of those imbedded in amber, is beset with many difficulties which make progress exceedingly slow, and which at times are responsible for no little discouragement. These obstacles are the direct result of the flattened condition of the insects, caused by the pressure of the strata above that containing the specimens. As the weight of these strata increases with the accumulation of sediment, the insects are pressed almost into a single plane. The disadvantage of this is obvious, for when the systematic position of a living insect is to be determined, the specimen must usually be examined in various positions and attitudes in order to reveal all the necessary characters. But since the fossil insect can be seen in just one position, only those characters visible in this position can be determined. The shape of the head, for example, can be used as a descriptive character only when the fossil shows a dorsal aspect. In the case of the ants this flattening is especially disconcerting, because the dorsal aspect of the head and a lateral view of the pedicel are nearly essential for the determination of the affinities of a species. Fortunately, there are a few structures, such as antennae and wings, which are visible in any attitude and are consequently the principle means of correlating the specimens in various positions.

* Extinct.

There are two types of distortions of the ants also resulting from flattening. The most obvious of these is the increase in the width of the specimen which takes place as the latter is pressed flat. The effect of this, of course, is to give the insect a more robust appearance than was characteristic of the ant when alive. Apparently the intensity of this pressure was very great, for the chitin of the head of many specimens is distinctly cracked just in front of the posterior angles, as in the holotype specimen of *Formica cockerelli*, sp. nov. (Plate 4, fig. 3). This splitting of the chitin occurs in precisely the same place, if a recent ant is pressed flat, and since it is always followed by a collapse of the entire head, which consequently becomes much broader, the presence or absence of the splitting indicates the degree of flattening which has taken place and provides a means of determining the original shape of the head. The second type of distortion is less evident, but equally noteworthy. It will be observed in most of the photographs of the Florissant species that the eyes are more remote from the lateral margins of the head than they are in the majority of living species. This is not a morphological peculiarity of the extinct species, but is merely due to the flattening of the head, and can be duplicated in recent forms by applying the necessary amount of pressure.

The application of a dilute solution of damar to the fossil has been found to improve the visibility of the insects nearly a hundred per cent. Many structures, especially the antennal segments and the veins of the wing, which could not otherwise be discerned in some specimens, become very distinct by the use of this medium. The resin hardens in a few hours, thus serving to protect the fossil from dust or scratches, and even from the cracking caused by the changes of atmospheric conditions. The hardened damar can easily be removed if desired, by soaking the specimen in xylol for a few days and then washing it for an equivalent time in absolute alcohol.

The Florissant ants are the only ones from American deposits which are sufficiently well preserved to permit determination of the generic affinities. Even the Green River shales, which have yielded a great number of splendidly preserved insects of other groups, have not produced a single satisfactory ant. My observations of the European fossil ants lead me to the conclusion also that those of Florissant are far better preserved than those of any other known deposit, excepting, of course, the Baltic amber. I have never seen a Radoboj or Oeningen ant with the eyes, antennae, or clypeus preserved, and very few of those described by Heer from those two localities show such details, as do the many of the Florissant specimens.

Only a small percentage of the ants in the collections at my disposal consist of both obverse and reverse. This is rather unfortunate, since the reverse is never the mirror image of the obverse. If, for example, a specimen is preserved in a dorso-lateral position, one half shows the structures as seen from above (eyes, clypeus, etc.) and the counterpart, only those visible from beneath (maxillae, etc.). This condition is well illustrated by the holotype of *Archiponera wheeleri*, sp. nov., of which the obverse is shown on Plate 1 and the reverse on Plate 2, fig. 1. When, however, the ant has been excessively crushed, as has frequently happened, the structures on the dorsal surface of the body may be faintly impressed on the ventral half. Of course, there are no structural differences in the halves of a fossil showing a lateral view of the ant, since the latter is bilaterally symmetrical.

Although the classification of living ants is based largely on workers, the poor representation of this caste among the fossils prevents us from following the same procedure in this study. As a consequence, I have substituted wherever possible the female for the worker as the important form of the species. The nature of the preservation of the ants has also required the selection of taxonomic characters somewhat different from those usually employed in the study of recent ants. The venation of the forewing is nearly indispensable for classification of the fossils, and inasmuch as the commonest castes are males and females, most of the specimens are winged. It is very essential, however, that venational characters be used with considerable caution, for in the ants as a whole the nature of the venation seems to be of little phylogenetic value. The arrangement of the veins in some of the highly specialized myrmicines, for example, is identical with that of certain primitive ponerines, yet the venation of two species within the same genus may be utterly different. Many ants, as *Lasius umbratus* (Adolf, 1880), have an exceedingly variable venation, and only a very few species, if any, have the shape of the cubital and discoidal cells exactly constant. It is not practical, therefore, to base a species on the micro-measurements of the sides of a cell, as Cockerell has done in his description of three ants from Florissant and a number of others from European deposits. There are some genera, however, which have the arrangement of the veins fairly constant and many of these are made distinctive by certain peculiarities which prove a great help in recognizing the genus—e.g., in *Myrmica* the apical half of the first intercubitus is always lacking. As far as the Florissant ants are concerned, the venation affords the best means of distinguishing the dolichoderines from the formicines, for the character ordinarily used to separate these

subfamilies, the shape of the cloaca, cannot be seen in the fossils. Venational studies have shown that if a member of one of these groups has two cubital cells, it is a dolichoderine; if it has only one cubital cell, it may belong to either subfamily.

The shape of the head, although somewhat distorted in most of the fossil ants, can nevertheless be used as a dependable character. In a large series of specimens of one species at least a few individuals are only very slightly flattened or distorted, and, even if all the specimens of a species are somewhat distorted, it is possible, as indicated above, to obtain a fairly accurate conception of the shape of the head. The mandibles are preserved in most of the Florissant specimens, often with sufficient completeness to show the details of the dentition. The clypeus is occasionally, but not frequently, visible at least to such an extent that the contour of the posterior margin can be determined. The antennae furnish the most reliable characters and this is especially advantageous because the same structure is likewise used in the classification of recent forms. The value of antennal characters in the fossils is also dependent upon the fact that the antennae are only a very little, if at all, distorted by the pressure which flattens the body of the insects. The length of the scape and the relative size of the funicular segments have been determined for nearly all of the Florissant ants, the only exceptions being a few aberrant forms which deserve description because of certain peculiarities. The eyes and even the ocelli have been discerned in most of the species, but it has already been explained above that the position of the eyes with respect to the lateral margins of the head is more or less dependent upon the amount of pressure to which the ant has been subjected. The color of the ants of the Florissant deposit does not usually indicate the original color of the insects and is of little use in identifying the fossil species. Brues has observed (1910) that the metallic colors of the parasitic Hymenoptera were clearly preserved in the Florissant specimens, but the pigmental colors of the ants appear to have been affected by the chemical activity which took place during the process of preservation of these insects. Individuals of a species vary from light brown to black, depending at least partly upon the rapidity of entombment, for the lighter specimens are usually much better preserved than the darker ones. There are, however, a few species, such as *Lasius peritulus* (Ckll.) and *Formica robusta*, n. sp., which are always brown, and since I have found this to be true for the hundreds of individuals of these two species which I have examined, it is very probable that the living ant was this same color. The relative size and qualitative dimensions of the

various parts of the ants are a necessary addition to the specific descriptions, and in the case of some males and a few workers, it has not been possible to give any other specific characters. Unless otherwise noted, the dimension given is the average of the results obtained from measurements of all the individuals of a species; only when a species has been found to be unusually variable are the two extremes indicated.

With some exceptions, each description of a new species is accompanied by a photograph of the holotype and a diagrammatic drawing of the ant. The photographs are essential to show the habitus of the fossils and will be of much assistance in the determination of material, although few details are visible in photographs of the size used. The drawings are not based upon any one specimen, except in the case of uniques, but are composite pictures containing all the characters which have been found in the specimens of the species illustrated. They are not, however, reconstructions in the usual sense of the term. The legs have been omitted from the figures, since they are not ordinarily well enough preserved for taxonomic purposes.

The preceding discussion has been made rather detailed in order to explain some of the problems encountered in this study, and the methods by which they have been partly, at least, overcome. This was considered advisable because the average entomologist appears to be skeptical of the results obtained by the study of fossil insects. The specialist who has for many years been determining his species by the distribution of hairs on the insect's head or the structure of the genitals naturally doubts the systematic value of the gross characters which are alone visible in the fossils, and consequently hesitates to accept the conclusions of the palaeoentomologist. Those who hold such an opinion have, I believe, overlooked the very significant fact that the study of fossil insects is essentially a division of palaeontology, rather than entomology. The palaeoentomologist is primarily concerned with the phylogeny of the insects, and whether or not one of the extinct forms has a little more pubescence on the abdomen than another is of very little consequence. If I have included under the name of *Formica robusta* two closely related species, differing only by the intensity of sculpturing on the clypeus, our conception of the geological history of the ants remains unchanged. The important fact is that the genus *Formica*, or even that a *Formica*-like genus, existed in Colorado during the Miocene.

The reconstruction of prehistoric life is always a slow process, whether we are concerned with the minute insect or the gigantic dinosaur. The picture of the earth's past is necessarily formed by the grad-

ual accumulation of fragments which, when placed together, make the whole. Just as the extinct reptile, at first known only by a single bone, is finally completely recognized by the addition of further material, so the fossil insect, originally represented by a wing or parts of the body, eventually becomes known to us in all details. And although the accumulation of the necessary specimens may be delayed for many years and the important details missing for an equivalent time, the results, on the whole, are dependable.

II. NORTH AMERICAN ANT DEPOSITS

Fossil ants have been found in five American localities:¹ the Green River formation of Colorado, Wyoming, and Utah; the Florissant shales of Colorado; the Elko oil shales of Nevada; the Quesnel clays of British Columbia; and the Fayette sandstone of Texas. The oldest of these, and in fact the oldest known ant deposit, is the Green River formation. This deposit has been known to be fossiliferous since the middle of the last century when John Evans collected a small fish in the beds near Green River, Wyoming. It was not until 1867, however, when the Hayden Geological Survey began a series of explorations of the Northwest Territories, that the fauna and flora of the shales were systematically studied. At that time Dr. F. V. Hayden, the director of the survey, named and described the deposit as follows (1873): "A little east of Rock Spring station [Wyoming] a new group commences composed of thinly laminated chalky shales, which I have called the Green River shales because they are best displayed along the Green River. They are evidently of purely fresh water origin and of middle Tertiary age. The layers are nearly horizontal and, as shown in the valley of Green River, present a peculiarly banded appearance. . . . The flora is already extensive, and the fauna consists of *Melania*s, *Corbula*s, and vast quantities of fresh water fishes. There are also numerous insects and other small undetermined fossils in the asphalt slates."

As these geological explorations continued, it became apparent that the same shales extended into Colorado, Utah, and other parts of Wyoming (Emmons, 1877; Endlich, 1878; Peale, 1876; White, 1878). In recent times more detailed studies on the geology of the formation have been made by Winchester (1923) and Bradley (1926). The shales were

¹ Since this paper was written (1928) a few ants have also been found in the Miocene (Latah) of Washington, and a single specimen has been collected in the Eocene (Wilcox) of Tennessee.

originally supposed to have been deposited by a large lake, some three hundred miles long and one hundred and fifty miles wide, and containing fresh water, as mentioned by Hayden in the description quoted above. Evidence accumulated within the past two years, however, indicates that the beds were formed by a number of small lakes, with a saline content at least part of the time (Bradley, 1926; Henderson, 1926; Cockerell, 1926).

Studies on the plants of the formation have determined the geological age as approximately middle Eocene. Knowlton (1922) in his excellent revision of the flora lists eighty-four species of plants and presents some interesting conclusions on the environment of the biota: "... It appears that an overwhelming preponderance of the living forms in the families represented in the Green River flora are inhabitants of tropical or subtropical regions, many of them in both hemispheres, yet a considerable number include either genera or species that extend into temperate regions. . . . The physical setting can be pictured somewhat as follows: about the shores of the lake were certain flat, low-lying areas, some of them probably swampy, others sandy, whereon grew the palms, figs, *Lomatia*, *Oreodaphne*, hackberries, the several papilionaceous trees and shrubs, the ferns, grass, sedge, etc., and in the water the pickerel weed, *Brasenia*, algae, etc. On the adjacent somewhat higher land might have been the willows, waxberries, sweet fern, walnuts, oaks, sumacs, maples (?), hollies, etc. . . . The conditions of temperature and moisture under which the Green River flora flourished are somewhat difficult of interpretation, as there is seemingly more or less conflict between the elements of the flora. The nearest living relatives of certain of the genera that are believed to have inhabited the lowlands . . . are found mainly in tropical and subtropical areas. The palms, at least one species of which existed in abundance, could hardly have lived where the temperature fell below 42° F. and probably not even where it was considerably higher than this. . . . The upland flora . . . could well have withstood some degree of frost, but on the other hand all these genera contain species that could find a congenial habitat in a warm temperate region. It is doubtful if any of them had to withstand cutting frosts."

The insect fauna of the formation contains nearly 300 described species and is not very different from that of the region at the present time. The abundance of the Fulgoridae, however, is rather striking, and Cockerell (1920) believes that these insects have a certain tropical appearance and resemble tropical genera. On the other hand, Alexander (1920) considers that the tipulid fauna is typical of that of the

north temperate region, so that the insects, as well as the plants, appear to show both tropical and temperate affinities.

The only other American Eocene deposit to yield fossil ants is at Mossy Creek, about three miles southwest of Wellborn, Brazos County, Texas. The beds, which belong to the Jackson series, consist at this outcrop of kaolinite lenses in sandstone, and contain twenty-four species of plants, including a common *Combretum* and the littoral palm, *Nipadites*. Professor E. W. Berry (1924) has concluded more or less tentatively, from his study of the flora, that the latter is indicative of a subtropical climate and a strictly coastal location. The insect fauna is very little known, only two species having been described.

The deposit at Quesnel, British Columbia, consists chiefly of fine grayish and greenish-white clays. The age of the formation is still somewhat uncertain, but the latest researches point to the Miocene (Reinecke, 1920). The flora is badly in need of revision, and since the insect fauna is a small one, nothing definite can be said of the climatic conditions under which the biota existed.

The two remaining ant deposits also belong to the Miocene and appear to be very similar as to fauna and flora. The smaller of these is the oil shale of Elko and its vicinity, in Nevada. No fossil insects have previously been described from this outcrop or, in fact, from any other rocks in the state, although the presence of insects has been recognized since Emmons's explorations during 1867-73. In his report on the geology of the region (1877) he states, "Adjoining the coal beds are fine bituminous shales, which closely resemble the brown paper shales of the Green River series at Green River City, Wyoming. In these are found the same plentiful remains of fishes, and also occasional insects." The geology of this bed was more carefully investigated by Winchester (1923), who states that "the shales . . . are in part clean clay shales but are mainly sandy. They usually lack sharp and distinct lamination and are generally interbedded with thin layers of muddy sandstone. In color they are commonly light gray, bluish gray, or brown. . . . Very thinly laminated paper shales are common at certain horizons." These strata have yielded a few fossil plants, which have been referred to the following genera (Knowlton, 1919): *Comptonia*, *Carpinus*, *Fagus*, *Ficus*, *Lycopodium*, *Myrica*, *Planera*, *Populus*, *Salix*, *Sapotacites*, *Sequoia*, and *Thuja*. Lesquereux, who first studied the flora, believed (1878) that the beds were the same age as those at Florissant, and Cope came to this conclusion from his studies on the fishes. At that time the Florissant shales were placed in the late Eocene or Oligocene, but further researches by Cockerell, Henderson, and Knowlton have

shown that they belong to the Miocene. In 1919 Knowlton definitely referred the Elko shales to this latter horizon, and this decision was later substantiated by the discovery of a Miocene mammal in the deposit (Winchester, 1923). The bed covers only a small area, not over thirty square miles, and appears to have been laid down by a fresh water lake under climatic conditions not unlike those which existed at Florissant during the Miocene. The only insects from this deposit which I have been able to locate are in the Museum of Comparative Zoölogy, and were collected by S. W. Garman in the thinly laminated paper shales about twenty miles northeast of the Elko station.

The other Miocene ant beds are the Florissant shales, which are located about thirty miles west of Colorado Springs, Colorado. Scudder's description of the location of the deposit is so admirable that I quote his own words: "By climbing a neighboring peak, thrice baptized as Crystal Mountain, Topaz Butte, and Cheops Pyramid, and known to the old miners as Slim Jim, we obtain an admirable view of the ancient lake and the surrounding region. To the southeast is Pike's Peak; to the west, South Park and the cañon of the South Platte, shown by a depression; to the extreme south the Grand Cañon of the Arkansas; while to the north a few sharp, ragged, granite peaks surmount the low wooded hills and ravines characteristic of the nearer region. Among these hills and ravines, and only a little broader than the rest of the latter, lies to the south, the ancient Florissant Lake basin, marked by an irregular L-shaped grassy meadow, the southern half broader and more rolling than the northwestern, the latter more broken and with deeper inlets." This deposit, which has produced more insects than any other known locality, was found to be fossiliferous by A. C. Peale in 1876. The geology and stratigraphy have been discussed in detail by a number of investigators, so only a brief survey of that aspect will be presented here. The upper part of the formation alone is fossiliferous, and this is composed of strata which vary much in thickness and composition, although for the most part volcanic ash, sand, and mud are the constituents. The shales apparently had their origin at the bottom of a lake, in the vicinity of which were a number of active volcanoes. The dust and ashes from the frequent eruptions of these volcanoes fell to the surface of the lake, carrying along the insects which happened to be flying or blown over the water, and quickly entombed them in a matrix of ash, sand and mud. Leaves of trees and shrubs, torn from their branches by violent winds and falling cinders, are exceedingly common in these shales. The flora of the deposit, which has been studied mainly by Lesquereux (1878, 1883), Kirchner (1878), Cockerell

(1908), and Knowlton (1917), includes such genera as *Acacia*, *Acer*, *Alnus*, *Amelanchier*, *Aster*, *Betula*, *Carpinus*, *Comptonia*, *Ficus*, *Fraxinus*, *Hicoria*, *Ilex*, *Juglans*, *Magnolia*, *Myrica*, *Pinus*, *Populus*, *Quercus*, *Rhamnus*, *Rhus*, *Rosa*, *Sabix*, *Sequoia*, *Smilax*, and *Ulmus*.

The insect fauna is exceptionally large, over a thousand species having been described, and seems to be modern in most respects. Both the insects and the plants suggest that the climate at the time of the deposition of the shales was similar to that of our southern states. Scudder has frequently observed that some of the insects have subtropical and even tropical affinities, and Cockerell has also called attention (1907) to a few genera which are now restricted to the old world (e.g. *Glossina*). The ant fauna shows this same geographical relationship.

III. THE EOCENE ANT FAUNA

1. The Green River formation, belonging to the Middle Eocene, contains the oldest ants known.¹ The only other ant deposits of Eocene age are the Bagshot beds, England, and the Fayette sandstone, Texas, both of which are somewhat younger than the Green River. The shales of this latter formation also have the distinction of being the first American rocks to produce Tertiary insects, one of the first specimens collected being an ant. In 1865, Professor William Denton, of Boston, discovered a series of Tertiary beds at the Junction of the Green and White Rivers, near the Colorado-Utah border (Fossil Cañon and Chagrin Valley). During the course of his examination of the petroleum shales which formed a part of the deposit, he found numbers of "Dipterous insects, especially mosquitos, and their larvae" (Denton, 1866). The insects were examined by Scudder who reported that the collection consisted of ninety specimens, representing sixty-five species, one of which belonged to *Myrmica*. This ant Scudder later concluded to be a dolichoderine, and described it as *Liometopum pingue*. Three years later, Dr. F. V. Hayden, who conducted many geological explorations into the Northwest Territories, found a few insects in a bed of these same petroleum shales which were exposed along a section ("Petriified Fish Cut") of the then recently built Union Pacific Railroad, at Green River City, Wyoming. Scudder studied these insects also, and stated that they belonged to "three species, one being an ant, the others flies. The ant is rather poorly preserved, and must be examined with great care before its precise characters can be determined." This species was

¹ An earlier ant, *Euponera berryi* Carp., has recently been found in the Lower Eocene of Tennessee. See Journ. Wash. Acad. Sci., 19, p. 300-301, 1929.

eventually described as *Lasius terreus*. During 1870 Scudder himself collected in these shales, both at the Wyoming and Utah exposures. In more recent times, ants have also been taken in this formation by Mr. Earl Douglass (1908, 1923), Mr. J. L. Kay (1923), Mr. Dean Winchester (1916), and Professor and Mrs. T. D. A. Cockerell (1922).

Although five supposed ants have been described from the Green River shales, only the one following is well enough preserved so that it can be placed in a subfamily with any degree of certainty. I am unable to add anything definite to the original description of the genus or species.

MYRMICINAE

ARCHIMYRMEX Cockerell

Cockerell, T. D. A., 1923. *Entomologist*, **56**, p. 51-52.

"Rather large, elongated ants, with a general resemblance to *Myrmecia*, but with the eyes (as in *Prionomyrmex*) high up on the side of the head; the epinotum with a distinct elevation (presumably pair of elevations), placed as in *Ectatomma tuberculatum*, but large and obtuse; mandibles less elongate, but still long, the cutting edge with coarse, obtuse teeth, between which are smaller ones; femora apparently shorter than in *Myrmecia*; first joint of pedicel elongated, with a dorsal elevation beyond the middle, the joint less massive than in the other two genera, but similar in principle to that of *Myrmecia vindex* Smith; second joint large and robust, quite like that of *Myrmecia*, as also the gaster."

Genotype.— *Archimyrmex rostratus* Ckll.

ARCHIMYRMEX ROSTRATUS Ckll.

(Plate 2, fig. 5)

Cockerell, T. D. A., 1923. *Entomologist*, **56**, p. 51-52.

Wheeler, W. M., 1928. *Soc. ins.*, p. 117.

"Worker: Color as preserved brown, the upper part of head and the gaster blackened, the coloration perhaps originally similar to that of *Myrmecia vindex* var. *nigriceps* Mayr. Length nearly 16 mm.; head with mandibles about 4 mm.; thorax about 5.3 mm.; middle femur about 3.7 mm."

Locality.— Roan Mountain, Colorado (Ute Trail).

Holotype.— Obverse, no. 15174, University of Colorado; reverse, no. 69617, U. S. N. M.

In his original description Cockerell regarded this ant as a ponerine, because of the apparent constriction at about the middle of the gaster. Wheeler, however, concluded (1928) from Cockerell's figure that "the specimen is more probably a Myrmicine. This is suggested by the shape of the petiole, the blunt or broken (?) spine on the epinotum and the shape of the head, which is unlike that of the existing Ponerinae." Through the kindness of Dr. R. S. Bassler I was able to study and photograph the reverse of the type at the National Museum. The obverse, at the University of Colorado, I was also permitted to examine, but was not able to secure a satisfactory photograph because of the lack of the necessary apparatus. My observations on these fossils did not aid materially in determining the affinities of the ant, although I believe that what appears to be an epinotal spine is merely the only part of the epinotum which is exposed to its dorsal surface, the adjoining parts of the epinotum being covered by the matrix of the rock. In as much as the specimen was a holotype, however, no attempt was made to test this conclusion by exposing the hidden part of the thorax. The habitus of the insect is certainly more suggestive of a myrmicine than a ponerine.

The two following Green River species, although unquestionably ants, are not sufficiently well known to permit even subfamily classification.

EOFORMICA PINGUE (Scudder)

(Plate 2, fig. 6)

Liometopum pingue, Scudder, S. H., 1877. Bull. U. S. Geol. Geogr. Surv. Terr., **3**, p. 742-743.

Liometopum pingue, Scudder, S. H., 1890. Bull. U. S. Geol. Surv., **13**, p. 617.

Eoformica eocenica, Cockerell, T. D. A., 1921. Proc. U. S. Nat. Mus., **59**, p. 38.

Eoformica eocenica, Wheeler, W. M., 1928. Soc. Ins., p. 117.

Male.—Length, 7.5 mm.; head small, nearly round, but somewhat broader behind; thorax broad, about twice as wide, and more than twice as long as the head; gaster rounded, about twice as long as the head and somewhat broader. Length of head, 1.2 mm.; thorax, 3.0 mm.; gaster, 2.7 mm. Width of head, 1.2 mm.; thorax, 2.2 mm.; gaster, 2.7 mm.

Locality.—Green River City, Wyoming; Rio Blanco County, Colorado; Uinta County, Utah.

Holotype.—No. 2937, M. C. Z.

This species was originally referred by Scudder to the genus *Liome-*

topum, but none of the known specimens are sufficiently well preserved to warrant this conclusion. In 1921 Cockerell described an ant (no. 66932, U. S. N. M.) from the Green River shales as *Eoformica eocenica*, for which he established a new genus. At the end of his description he suggested that this species might be identical with Scudder's *Liometopum pingue*, and my comparison of the two types shows that this really is the case. Cockerell attempted a restoration of the frontal view of the head of this species, although the only specimen which he saw presented a lateral aspect of the insect. Through the courtesy of the National Museum I was able to make a careful study of the fossil which Cockerell used as the basis of this restoration, but could not discern any definite indications of the eyes or mandibles shown in his figures. If either of Cockerell's drawings (which do not agree in certain details) represent the true characteristics of the ant, the species can have only the remotest affinities with *Formica* or *Liometopum*.

Regardless of the vague relationships of this insect, there are several noteworthy features associated with it. Although none of the other Green River ants is known from more than a single specimen, I have seen twenty-six individuals of *E. pingue*, all of which are males. The wide distribution over the various outcrops of the Green River formation is also remarkable. Scudder's specimens were collected at Fossil Cañon, White River, Utah (Denton), and Green River, Wyoming (Packard); and the one described by Cockerell as *Eoformica eocenica*, at Cathedral Bluffs, Colorado. The additional fossils which I have examined represent the following localities: Wagon Hound Cañon, Uinta County, Utah (Douglass); White River Cañon, Uinta County, Utah (Kay); White River, Uinta County, Utah (Douglass); Roan Mountains, Rio Blanco County, Colorado (Winchester and Cockerell); Dripping Rock Cañon, Rio Blanco County, Colorado (Douglass); and Green River, Wyoming (Winchester). If the species were not so common at the localities mentioned, which are spread over an area of about 34,000 miles, one might easily assume that the relative abundance of individuals was due to the drowning of a number of specimens of a single nuptial flight, which happened to be directed over the lake. But the regular occurrence of the species over so large an area is conclusive evidence that this ant was in reality the commonest in the vicinity of the Green River lakes. That the species also existed in the region for a long period is evinced by the presence of specimens at various levels of the shales, which at some exposures exceed a thousand feet in thickness.

(FORMICIDAE) TERREUS (Scudder)

Lasius terreus, Scudder, S. H., 1878. Bull. U. S. Geol. Geogr. Surv. Terr., **4**, p. 747-748.

Lasius terreus, Scudder, S. H., 1890. Bull. U. S. Geol. Surv. Terr., **13**, p. 618; pl. 10, fig. 23.

Worker (?).—Length, 7.5 mm.; “head small, rounded, with antennae shaped as in *Lasius*, but of which the number and relative length of the joints cannot be determined from their obscurity; the long basal joint, however, appears to be comparatively short and of uniform size, being not quite so long as the width of the head, while the rest of the antenna is more than half as long as the basal joint and thickens very slightly near the apex. The thorax, preserved so as to show more of a dorsal than a lateral view, is compact, oval, less than twice as long as broad, with no deep separation between the meso- and metathorax, tapering a little posteriorly. The peduncle, as preserved, is a minute circular joint, but from its discoloration appears to have had a regular, rounded, posterior eminence. The abdomen consists of five joints, is very short, oval, compact and regular, and of about the size of the thorax, although rounder.” Length of head, 1.4 mm.; thorax, 3.3 mm.; gaster, 3.0 mm. Width of head, 1.0 mm.; thorax, 1.9 mm.; gaster, 2.2 mm.

Locality.—Green River City, Wyoming.

Holotype.—No. 69618 U. S. N. M.

The single specimen of this species is very poorly preserved, and since I have not been able to discern in the type many of the characters given by Scudder in the description quoted above, it is very probable that the fossil has deteriorated since Scudder's examination of it. The assignment of this species to *Lasius* or any other existing genus will not be justified until additional specimens have been found.

The two following Green River insects described by Scudder as ants do not really belong to the family, but apparently to some other groups of aculeate Hymenoptera:

“MYRMICA SP.” Scudder

Scudder, S. H., 1878. Bull. U. S. Geol. Geogr. Surv. Terr., **4**, p. 748.

“CAMPONOTUS VETUS” Scudder

Scudder, S. H., 1877. Bull. U. S. Geol. Geogr. Surv. Terr., **3**, p. 742.

In addition to the preceding fossils I have seen four other ants from the Green River formation, collected by Mr. Earl Douglass in Uinta

County, Utah. One of these, an isolated specimen, is possibly a ponerine queen; the remaining three, which are close together on a small slab of the shale, seem to belong to different genera, but they are so poorly preserved that their generic affinities cannot definitely be ascertained. At any rate, these four species, together with the three discussed above, are sufficient to show that the ant fauna of the Middle Eocene was essentially a modern one, at least to the extent that several of the living families were already established and the castes differentiated.

2. The kaolinite of the Jackson formation (Upper Eocene) has yielded a single, splendidly preserved forewing of an ant.

(FORMICIDAE) EOPTERA (Ckll.)

Formica eoptera, Cockerell, T. D. A., 1923. Amer. Journ. Sci., 5 (29), p. 399-400.

"Anterior wing, 11 mm. long and 4 wide; hyaline, faintly reddish, with pale but stout veins; stigma lanceolate, slender; costal cell very slender; basal nervure with upper section only slightly out of straight line with lower, the lower distinctly but not much longer; nervulus about 1.6 mm. basal of basal nervure; discoidal cell large, subquadrate, but narrower above than below, and apically broader than basally, the upper basal corner obtuse; marginal cell long and broad, its inner corner acute; marginal and cubital nervures forming a cross as in *Camponotus*."

Locality.—Mossy Creek, Brazos County, Texas.

The holotype of this insect appears to be lost; it is not recorded at the National Museum, where the rest of Professor Berry's types are located.

As Wheeler has already pointed out (1928), a generic determination of this ant is impossible.

IV. THE MIOCENE ANT FAUNA

1. The ant fauna of the Quesnel clays (Fraser Formation) is even more fragmentarily known than that of Green River; only four specimens have been found and these are so poorly preserved that very little can be said of their affinities. The species represented by these fossils were described by Scudder, three of them as ants and the fourth as a brachonid.

(DOLICHODERINAE) OBLITERATA (Scudder)

Hypoclinea obliterata, Scudder, S. H., 1877. Rep. Progr. Geol. Surv. Can., 1875-76, p. 267.

Hypoclinea obliterata, Scudder, S. H., 1890. Bull. U. S. Geol. Surv., **13**, p. 616, pl. 3, fig. 25, 26.

The specimen from which this ant was described consists only of the gaster, the posterior half of the thorax, and a forewing. Since the pedicel is apparently single jointed and the wing has two cubital cells, the species is probably a dolichoderine, but there is no evidence whatever that it belongs to Dolichoderus.

Holotype.— Obverse, no. 6179, Canadian Geological Survey; reverse, no. 2938, M. C. Z.

(MYRMICINAE) LONGAEVA (Scudder)

Aphaenogaster longaeva, Scudder, S. H., 1877. Rep. Progr. Geol. Surv. Can., 1875-76, p. 267.

Aphaenogaster longaeva, Scudder, S. H., 1890. Bull. U. S. Geol. Surv., **13**, p. 61, pl. 13, fig. 24.

The forewing and some parts of the body are preserved; the pedicel is typically myrmicine, but no generic determination can be made.

Holotype.— Obverse, no. 6178, Canadian Geological Survey; reverse, no. 2939, M. C. Z.

(FORMICIDAE) ARCANA (Scudder)

Formica arcana, Scudder, S. H., 1877. Rep. Progr. Geol. Surv. Can., 1875-76, p. 266-67.

Formica arcana, Scudder, S. H., 1890. Bull. U. S. Geol. Surv., **13**, p. 618, pl. 13, fig. 24.

This ant is represented by a forewing, possessing a cubital and discoidal cell, and consequently might belong to any one of a number of genera.

Holotype.— No. 6180, Canadian Geological Survey.

(FORMICIDAE) ANTEDILUVIANUM (Scudder)

Calypptiles antediluvianum, Scudder, S. H., 1878. Rep. Progr. Geol. Surv. Can., 1876-77, p. 270.

Calypptiles antediluvianum, Wheeler, W. M., 1908. Journ. f. Psych. u. Neurol., **13**, p. 417.

This species, based on one specimen consisting of a forewing, was originally described by Scudder as a braconid, but it is really a formicid with uncertain generic affinities.

Holotype.— Canadian Geological Survey.

2. The oil shales at Elko, Nevada, have contributed one fossil ant, which, although poorly preserved and much distorted, is nevertheless described below because it represents a new locality for the family, and even for the insects as a whole.

FORMICINAE

PSEUDOCAMPONOTUS, gen. nov.

Similar to *Camponotus* but with the eyes and antennal insertions farther forward on the head; antennae consisting of twelve segments in the female.

Genotype.— *Ps. elkoanus*, sp. nov.

PSEUDOCAMPONOTUS ELKOANUS, sp. nov.

Plate 2, fig. 2

Female.—Length, 7.0 mm. Head quadrate, a little longer than broad; mandibles massive, triangular; clypeus large, the anterior border with a small tooth on each side of a median notch, the posterior margin with a lobe extending back nearly to the middle of the head; eyes small, situated at about the middle of the sides of the head; scape just reaching the posterior margin of the head, slender; funicular segments subequal, about as long as broad; thorax about as long and as broad as the head; petiole apparently rather wide; gaster small, only a little longer than the head, rounded. Length of head, 1.8 mm.; scape, 1.22 mm.; funiculus, 1.8 mm.; thorax, 2.0 mm.; gaster, 2.4 mm.; forewing, 6.0 mm. Width of head, 1.3 mm.; thorax, 1.2 mm.; gaster, 2.0 mm.

Locality.— Near Elko, Nevada, "20 miles or more northeast from the station, from a shaft sunk by the Central Pacific Railroad Company." (S. W. Garman).

Holotype.— No. 2940, M. C. Z.

The obscurity of the petiole and venation of this species prevents the generic affinities from being accurately determined. The habitus is nearest to that of the Camponotini, with the exception of the position of the eyes and the antennal insertions, so that until additional material

has been found the species had probably best be assigned to a new genus within this tribe. Professor Wheeler has suggested to me that the prolongation of the clypeus gives somewhat the appearance of the truncated head of the subgenus *Colobopsis*, and this character would agree with the structure of the mandibles as indicating that the ant was a wood-inhabiting species.

The Florissant shales have produced more fossil ants than any of the other deposits, excepting, of course, the Baltic amber. Scudder remarks in his volume on the Tertiary insects of North America that "the ants are the most numerous of all the insects at Florissant, comprising, perhaps, a fourth of all the specimens; they form more than three-fourths, perhaps four-fifths, of all the Hymenoptera; I have already about four thousand specimens of perhaps fifty species (very likely many more)." Some four thousand additional specimens were obtained by the expeditions conducted after 1900, and Mr. S. A. Rohwer tells me that a great number of poorly preserved ants were discarded at the locality. Still further evidence of the abundance of the ants at the time of the existence of the Florissant biota is afforded by the presence of many specimens of fossil fish excrement; apparently consisting of the "hard, indigestible heads of ants" (Wheeler, 1910).

About half of the 12,000 specimens which I have examined are well enough preserved to permit specific determination, and nearly a half of the remainder show details sufficient for generic diagnosis. By far the majority of the specimens are males and females, which are nearly equally represented; only about two per cent. are workers. This scarcity of neuters is obviously due to their inability to fly over the lake, for since only a relatively few specimens were blown from the trees or shrubs into the water, they were rarely preserved as fossils. The same deficiency of workers was observed by Heer in his study of the ants in the Oeningen beds, in which "mit einigen wenigen Ausnahmen finden sich nur geflugelte Individuen vor, weil die ungeflugelten Thiere, hier also die geschlechtslosen Individuen, viel seltener im Wasser verungluechten, als die ersteren." The opposite tendency is naturally found in the Baltic amber fauna, most of which "are workers and belong to more or less arboreal species, but there are also quite a number of males and females. As nearly all of the latter have wings, they must have been caught in the liquid resin just before or after the nuptial flight." (Wheeler, 1910.)

The correlation of the castes of the Florissant ants is very difficult. This is especially so because the females and males of a species do not usually occur even in an approximately equal abundance. The com-

monest female, for example, is that of *Protazteca elongata*, sp. nov., while the most abundant male is that of *Lasius peritulus* (Ckll.). An even better illustration is afforded by *Miomymex impactus* (Ckll.) and *M. striatus*, sp. nov., the former of which is represented by thirty-seven females and one male, and the latter by two females and fifteen males. The determination of the affinities of the males has been exceedingly troublesome, partly because this caste has been so little used in the taxonomy of existing ants, and partly because of the slight generic differentiation of this sex.

The number of species of Florissant ants was estimated by Scudder to be close to fifty, but this is considerably more than the actual amount. Thirty-two species are described below and although a few others may turn up in later collections, the total number will probably not exceed forty. These species are distributed among five of the seven recognized subfamilies. The following list shows the abundance of the species, and the table summarizes the ant faunas of the Florissant shales and the Baltic amber, so that they may be easily compared.

Name	Sexes known	No. of Specimens
<i>Archiponera wheeleri</i> , sp. nov.	♀ ♂	2
<i>Pseudomyrma extincta</i> , sp. nov.	♀	2
<i>Aphaenogaster mayri</i> , sp. nov.	♀ ♂	200
<i>Aphaenogaster donisthorpei</i> , sp. nov.	♀	1
<i>Pheidole tertiaria</i> , sp. nov.	♀	2
<i>Messor sculpturatus</i> , sp. nov.	♀	20
<i>Pogonomyrma fossilis</i> , sp. nov.	♀	1
<i>Lithomyrma rugosus</i> , sp. nov.	♂ ♀	40
<i>Lithomyrma striatus</i> , sp. nov.	♀	2
<i>Cephalomyrma rotundatus</i> , sp. nov.	♀	1
<i>Mianeuretus mirabilis</i> , sp. nov.	♀	1
<i>Dolichoderus antiquus</i> , sp. nov.	♀ ? ♀	10
<i>Dolichoderus rohweri</i> , sp. nov.	♀ ♀	7
<i>Protazteca elongata</i> , sp. nov.	♀ ♂ ♀	1,500
<i>Protazteca quadrata</i> , sp. nov.	♀ ♀	50
<i>Protazteca capitata</i> , sp. nov.	♀ ? ♀	30
<i>Liometopum miocenicum</i> , sp. nov.	♀ ♂ ♀	1,500
<i>Liometopum scudderi</i> , sp. nov.	♀ ♀	200
<i>Elaeomyrma gracilis</i> , sp. nov.	♀ ♀	50
<i>Elaeomyrma coloradensis</i> , sp. nov.	♀ ♀	29
<i>Iridomyrma florissantius</i> , sp. nov.	♀ ♀	34
<i>Iridomyrma obscurans</i> , sp. nov.	♀ ♀	26
<i>Miomymex impactus</i> (Ckll.)	♀ ♂ ♀	38
<i>Miomymex striatus</i> , sp. nov.	♂ ♀	17

Name	Sexes known	No. of Specimens
<i>Petraeomyrmex minimus</i> , sp. nov.	♀	11
<i>Formica robusta</i> , sp. nov.	♂ ♀	400
<i>Formica cockerelli</i> , sp. nov.	♂ ♀	5
<i>Formica grandis</i> , sp. nov.	♀	1
<i>Lasius peritulus</i> (Ckll.)	♂ ♀	1,400
<i>Camponotus fuscipennis</i> , sp. nov.	♀	4
<i>Camponotus microcephalus</i> , sp. nov.	♀	1
<i>Camponotus petrifactus</i> , sp. nov.	♂	7

FLORISSANT

Subfamily	Extinct genera	Extant genera	Species	Individuals
Ponerinae	1	0	1	2
Pseudomyrminae	0	1	1	2
Myrmicinae	2	4	8	267
Dolichoderinae	5	4	15	3,505
Formicinae	0	3	7	1,818
	8	12	32	5,594

BALTIC AMBER

Subfamily	Extinct genera	Extant genera	Species	Individuals
Ponerinae	3	4	8	106
Cerapachinae	1	0	2	6
Pseudomyrminae	0	1	5	18
Myrmicinae	7	7	25	214
Dolichoderinae	4	3	20	7,508
Formicinae	5	8	32	3,827
	20	23	92	11,679

From these tables it is obvious that the subfamily Dolichoderinae is the predominant one of the Florissant ant fauna in all respects— numbers of genera, species and individuals. The Formicinae rank second as to the number of individuals present, but are exceeded by the Myrmicinae in the number of genera and species. It will be noted that in the amber fauna the Dolichoderinae lead only as to the number of individuals, the Myrmicinae as to the number of genera, and the

Formicinae as to the number of species. The large number of dolichoderine individuals in the amber is due, however, to the excessive abundance of one species, *Iridomyrmex goepperti* Mayr, of which 5,428 specimens have been found.

It is also evident from the foregoing list that on a basis of their geographical distribution the genera of Florissant ants (excepting those extinct ones whose affinities are not recognized) may be divided into three groups:

1. Those now present in Colorado or neighboring states. As one would expect most of the genera fall within this category, as *Pseudomyrma*, *Pheidole*, *Aphaenogaster*, *Pogonomyrmex*, *Liometopum*, *Iridomyrmex*, *Formica*, *Lasius*, and *Camponotus*.

2. Those which represent a definite neotropical element. Here belong *Archiponera*, gen. nov. (affin. *Dinoponera*) and *Protazteca*, gen. nov. (affin. *Azteca*).

3. Those which represent the old-world fauna, as *Messor* and *Mianeuretus*, gen. nov. (affin. *Aneuretus*).

The significance of this combination of faunas will be discussed later, but it might be noted here that the Baltic amber ants as well are "a mixture of what at the present day we are able to recognize as at least four different faunas, the palearctic, the Indian, the Malayan, and the Australian, with a little more than one-third the genera and nearly one-half of the species palearctic and the remainder belonging to Indomalayan and Australian types." (Wheeler, 1914.)

Comparing the relative numbers of extinct and living ant genera in the amber and Florissant shales, it is interesting to note that 44.1% of the former, and 40% of the latter are extinct. This close agreement is about what should be expected in view of the short interval of time between the Oligocene and the Miocene. It is also instructive to compare the relative number of extinct genera in the other groups of Florissant insects which have been sufficiently well treated. Of the parasitic Hymenoptera, which were studied by Professor C. T. Brues (1910), about 13% of the genera are no longer living. The great difference between this percentage and that of the ants is probably largely due to the fact that in determining the affinities of the fossils Professor Brues was obliged to consider the genera in a somewhat broader sense than has been done with the ants. The Coleoptera, which have been studied very thoroughly by Professor H. F. Wickham, are mainly represented by living genera also, less than 20% being extinct. This is not surprising, however, if we bear in mind that this order is geologically much older than the Hymenoptera, and that many of the living families were well established during the Triassic.

PONERINAE

The Florissant collection contains but a single recognizable species of this subfamily. There are two poorly preserved male ants in the Scudder material which may possibly belong here also, but they are too obscure for description. Cockerell has described a species which he placed in *Ponera* (1906) and later in *Euponera* (1927), but this ant is really a dolichoderine and will be discussed under the new genus *Protazteca*.

PONERINI

ARCHIPONERA, gen. nov.

Allied to *Dinoponera* and *Streblognathus*.

Worker.—Head large, with convex sides and broadly rounded posterior angles; mandibles small, linear; clypeus large, anterior margin with a median incision, posterior margin with a large median lobe; eyes small, situated very high up on the sides of the head, a little posterior of the middle line of the head; ocelli absent; antennae long and slender, twelve-jointed; petiole short but high, cuneiform; gaster small, globular, the first two segments of moderate size, the others short and compressed.

Male.—Slender; petiole long, with a low scale; forewing with two cubital cells, the first intercubitus joining the cubitus at a point much above the junction of the latter with the recurrent vein; second intercubitus far apical of the termination of the first intercubitus.

Genotype.—*Archiponera wheeleri*, sp. nov.

ARCHIPONERA WHEELERI, sp. nov.

Plate 1. Plate 2, fig. 1

Worker.—Length, 15.0 mm. Head nearly round, as broad as long; posterior margin slightly concaved; scapes greatly exceeding the posterior margin of the head; first six and last funicular segments about twice as long as broad, the others only about as long as broad; thorax as long as the head, but only a little more than half as broad; gaster only a very little longer than the head, and not as wide. Length of head, 4.5 mm.; scape, 3.0 mm.; funiculus, 4.0 mm.; thorax, 4.5 mm.; gaster, 5.0 mm. Width of head, 4.5 mm.; thorax, 2.3 mm.; gaster, 3.0 mm.

Holotype (♀). — No. 2876a-b, M. C. Z. (S. H. Scudder).

The specimen on which this species is based is an example of the remarkable preservation which occasionally occurs among Florissant fossils. Not only are the minute structures preserved in detail, but the whole insect stands out in such strong relief that the dorsal outline of the body can be ascertained by regarding the fossil from the side. There is not the slightest indication of distortion, the insect being perfectly symmetrical, in a normal, straight position, so that from the photograph one could easily imagine that the figure had been engraved on the rock. The existence of such strong relief is, of course, proof that distortion by flattening has been reduced to a minimum. It will be observed, however, that this conclusion is apparently contrary to the evidence afforded by the remoteness of the eyes from the lateral margins of the head, for, as was shown above, this condition usually results from flattening. This contradiction is at once removed and additional proof of the systematic position of the ant is furnished by comparing extant species of *Streblognathus*, *Dinoponera*, and allied genera, for in these forms the eyes are actually on the dorsal surface of the head rather than the sides, and from a dorsal aspect appear in precisely the same position as they do in the fossil. It will be observed also that only the first two gastric segments appear to be preserved, but a careful examination of the reverse of the specimen reveals the remaining segments compressed together and curled under the second segment. This is a condition frequently found in specimens of *Dinoponera*, which from a dorsal view show only the first two segments.

The constriction between the first and second gastric segments is very marked (see Plate 2), leaving no question that this ant is a ponerine. The linear mandibles, the form of the clypeus and petiole, as well as the characters mentioned above, place it very close to *Dinoponera* and *Streblognathus*. It differs from each of these genera in the more rounded head, and also by the lack of the blunt tooth on the sides on the median emargination of the anterior margin of the clypeus.

Inasmuch as the female of *Streblognathus* or *Dinoponera* is not known, I hoped to find the queen of *A. wheeleri*, sp. nov., in the Florissant collection, but only the male turned up. Unfortunately, the head of this latter specimen is not preserved, apparently having been separated from the thorax before the insect was entombed in the mud at the bottom of the lake. Nevertheless, there are sufficient details present to associate definitely this fossil with the above worker. The male has the following characteristics: length, 13.0 mm. Petiole large, the node with a long anterior face (indicated in relief); gaster long and slender; venation nearly identical with that of *Dinoponera grandis*. Length of

thorax, 5.0 mm.; gaster, 7.0 mm.; forewing, 6.00. Width of thorax and gaster, 3.0 mm.

Allotype.—No. 2877, M. C. Z. (W. P. Cockerell).

It will be seen from the above description that the male is much smaller than the worker. This is the reverse of the usual condition in the ants, but is true of *Dinoponera grandis* (Guerin), the worker of which is about 26.0 mm. long and the male only 18.0 mm. The petiole of the male has quite the same appearance as that of *D. grandis* when viewed from above. The venation is of a peculiar, primitive type, found only in such ponerine genera as *Paltothyreus*, *Dinoponera*, *Streblognathus*, and *Myrmecia*.

The occurrence of such a ponerine as this in the Miocene of Colorado is of considerable interest in connection with the geographical distribution of *Streblognathus* and *Dinoponera*, its nearest relatives. Both of these extraordinary genera are monospecific, *S. aethiopicus* (F. Smith) occurring in South Africa, and *D. grandis* (Guerin) in South America. Although these two species are placed in separate genera, distinguished by the structure of the claws and the shape of the petiole, they are closely enough related so that we may regard them as a compact group and representing a supergenus, which during the Pleistocene and perhaps postglacial times was tropicopolitan, and which during the Tertiary extended further northward, where it was represented by *Archiponera wheeleri*, sp. nov., and probably other forms still unknown.

PSEUDOMYRMINAE

This subfamily, consisting of one tribe, Pseudomyrmini Forel, includes a few tropical and subtropical species belonging to four genera. Three of these, *Pachysima*, *Viticiola*, and *Tetraponera* are confined to the old world, the latter genus alone extending as far north as Palestine. *Pseudomyrma* itself is the only genus which occurs in the New World, and this reaches as far north as Texas and Florida. In the Tertiary, however, the subfamily was much more widely distributed, as evinced by the presence of five species in the Baltic amber belonging to *Tetraponera*, and one species of *Pseudomyrma*, described below, from the Florissant shales.

PSEUDOMYRMA, Latr.

PSEUDOMYRMA EXTINCTA, sp. nov.

Plate 3, fig. 4

Female.—Length, 9.0 mm. Slender, head elongate-oval, with a short posterior margin and curved lateral margins; scapes very short,

about one-half the length of the head; thorax about as long and as wide as the head; petiole and postpetiole attenuate, the petiole longer and narrower than the postpetiole; gaster slender, nearly two and one-half times as long as the head, but only a little wider; forewing not exceeding the end of the gaster, with two cubital cells. Length of head, 1.8 mm.; thorax, 2.0 mm.; pedicel, 1.2 mm.; gaster, 4.2 mm.; forewing, 5.0 mm. Width of head and thorax, 1.2 mm.; gaster, 1.8 mm.

Holotype.— No. 2899, M. C. Z. (S. H. Scudder).

Paratype.— No. 2900a-b, M. C. Z. (S. H. Scudder).

The holotype, an obverse, appears to be dealated. The species is very rare, only the two types being known.

MYRMICINAE

PHEIDOLINI

APHAENOGASTER Mayr

This widely distributed genus is represented in the Tertiary formations by three species in the Baltic amber, two in the Radoboj beds, and the three following in the Florissant shales. Scudder's *Aphaenogaster longaeva*, from Quesnel, B. C., cannot be referred to this genus, as shown above.

APHAENOGASTER MAYRI, sp. nov.

Plate 5, fig. 5. Plate 8, fig. 4. Plate 9, fig. 5. Plate 11, fig. 4.

Female.— Length, 7.0–8.0 mm. Moderately slender; head rather small, longer than broad; posterior margin straight; mandibles large, well developed; scape rather long and slender, exceeding the posterior margin of the head; funicular segments 3–8, about one and one-half times as long as broad, segments 2, 9, 10 a little more than twice as long as broad, and the last segment three times as long as broad; thorax longer than the head and a little broader; epinotum with a pair of short but distinct spines; petiole more or less pedunculate, longer than the post-petiole; gaster small, about one and one-half times the length of the head and about as wide; in many specimens the second and subsequent segments of the gaster are compressed, so that the abdomen seems much smaller. Sculpturing on head and thorax usually distinct. Length of head, 2.1 mm.; scape, 1.5 mm.; funiculus, 2.1 mm.; thorax, 2.5 mm.; gaster, 3.0 mm. Width of head, 1.5 mm.; thorax 1.8 mm.; gaster, 1.5 mm.

Holotype (♀).— No. 2949, M. C. Z. (S. H. Scudder).

Paratypes (♀).—Nos. 2942, 2901–2912, M. C. Z.; no. 1030, Peabody Museum, Yale University; nos. 7845–7849, Princeton University; no. 17016a, Colorado University; no. 78,803, U. S. N. M.; no. 22,966, A. M. N. H.; nos. 36–43, Wickham coll.; no. 10, Carnegie Museum; no. (1), British Museum.

Male.—Length, 6.0 mm. Similar to the female, but with a smaller, more nearly triangular head; funicular segments about twice as long as broad; venation as in the female. Length of head, 1.2 mm.; scape, 0.6 mm.; funiculus, 1.8 mm.; thorax, 1.8 mm.; gaster, 1.8 mm. Width of head, 0.7 mm.; thorax, 0.9 mm.; gaster, 1.5 mm.

Allotype (♂).—No. 2914, M. C. Z.; no. 10031, Peabody Museum; no. 17016b, University of Colorado; no. 78,803, U. S. N. M.

Worker.—Very similar to the female, but smaller, with heavier sculpturing on the head. Length, 6.0 mm.; length of head, 1.5 mm.; scape, 1.1 mm.; funiculus, 2.0 mm.; thorax, 2.0 mm.; gaster, 2.4 mm.

Ergatotype.—No. 2915, M. C. Z. (S. H. Scudder).

Paratypes (♀).—No. 2916, M. C. Z.; no. 17,016c, University of Colorado; no. 78,803, U. S. N. M.

This species, the commonest myrmicine in the Florissant shales, is represented in the material which I have examined by some two hundred good specimens, nearly all of which are queens. The sculpturing on the female is usually discernible, and in some specimens is preserved with remarkable clearness, as in paratype no. 2912a (see Plate 8, fig. 4).

APHAENOGASTER DONISTHORPEI, sp. nov.

Plate 7, fig. 4

Female.—Length, about 7.0 mm. Slender; head much longer than broad, elongate-oval; antennae long and slender, the scape greatly exceeding the posterior margin of the head; funicular segments about twice as long as broad; thorax longer than the head, but only about as wide; forewing exceeding the end of the abdomen; venation similar to that of *Aphaenogaster mayri*, sp. nov. Length of head, 1.9 mm.; scape, 1.8 mm.; funiculus, 2.1 mm.; thorax, 2.5 mm.; forewing, 6.0 mm. Width of head and thorax, 1.2 mm.

Holotype.—No. 2917, M. C. Z. (S. H. Scudder).

This species is described from a single specimen, which, although not very well preserved, shows sufficient characters to distinguish it from the other Florissant species. It is much more slender than *A. mayri*, and the scape, head, and thorax are relatively longer.

MESSOR Forel

This genus, which is now restricted to the tropical and palaeartic regions of the Old World, is represented in the Florissant beds by a fairly common species. The recent genera, *Novomessor* Emery and *Veromessor* Forel are the closest American relatives of *Messor*, but are distinguished from it by the forewing, which has two cubital cells in *Messor* and only one in *Novomessor* and *Veromessor*. The Florissant species, having two closed cubital cells in the forewing, cannot belong to either of the American genera, unless we consider it as representing a new and aberrant subgenus. However, inasmuch as there are no characters sufficient to separate it from *Messor*, it seems advisable to place it within this latter genus. This conclusion seems especially justified in view of the occurrence of other Old World genera in the Florissant shales (e.g. *Glossina*).

MESSOR SCULPTURATUS, sp. nov.

Plate 4, fig. 5. Plate 11, fig. 5

Female.—Length, 10.0 mm. Robust; head large, posterior margin slightly curved, lateral margins a little convex; mandibles well developed; antennae slender, scape reaching the posterior margin of head; funicular segments 3–10 somewhat longer than broad, segments 2, 11, 12 about twice as long as broad; thorax much longer than the head but only about as wide; petiole and postpetiole nearly equal in height, the petiole somewhat longer; gaster small, about one and one-half times as long as the head, but only as wide; forewing exceeding the tip of the gaster. Head, thorax, and petiole with fine, but distinct striations. Length of head, 2.4 mm.; scape, 1.8 mm.; funiculus, 2.2 mm.; thorax, 2.4 mm.; gaster, 3.7 mm.; forewing, 7.0 mm. Width of head, 1.9 mm.; thorax, 1.8 mm.; gaster, 1.8 mm.

Holotype (♀).—No. 2920, M. C. Z. (S. H. Scudder).

Paratypes (♀).—No. 2921, M. C. Z.; no. 10,032, Peabody Museum; no. 7850, Princeton University; no. 17,017a, University of Colorado; no. 78,804, U. S. N. M.; no. 11, Carnegie Museum.

The holotype specimen is very faint, but well preserved. In all, twenty individuals of this species have been found.

PHEIDOLE Westwood

This genus has not previously been recorded from Tertiary strata, although it has a wide and primitive distribution in the tropical, ne-

arctic, and southern palaeartic regions. In the Florissant collection I find two splendid specimens of a single species.

PHEIDOLE TERTIARIA, sp. nov.

Plate 5, fig. 2. Plate 11, fig. 2

Female.—Length, 7.0 mm. Head large, nearly as broad as long, narrowed anteriorly; posterior margin slightly incised; mandibles well developed; antennae situated rather far forward; scapes slender, reaching the posterior margin of the head; funiculus moderately slender, segments 2-9 a little longer than broad, the last three segments enlarged to form a club; eyes small, situated very nearly at the middle of the sides of the head; ocelli unusually large; thorax about as long as the head, but not quite as wide; epinotum (apparently) unarmed; petiole and postpetiole short, but probably quite high; gaster small, as long as the head, and about as wide; forewing extending much beyond the end of the gaster. Head coarsely and reticulately rugose; mesonotum and metanotum also rugose, but not so distinctly. Length of head, 2.3 mm.; scape, 0.12 mm.; funiculus, 2.4 mm.; thorax, 2.3 mm.; gaster, 2.5 mm. Width of head, 1.8 mm.; thorax, 1.6 mm.; gaster, 1.8 mm.

Holotypes.—No. 2918, M. C. Z. (S. H. Scudder).

Paratypes.—No. 2919, M. C. Z.

Both types are well preserved and are obverses, showing the dorsal aspect of the ant. Since there is no indication of epinotal spines in either specimen, I have concluded that the thorax was unarmed, as in *Ph. guilemi-muelleri* Forel.

MYRMICINI

POGONOMYRMEX Mayr

This neotropical and nearctic genus, of which two species now occur in Colorado, is represented for the first time in the Tertiary by one species in the Florissant beds.

POGONOMYRMEX FOSSILIS, sp. nov.

Plate 9, fig. 6

Worker.—Length, 6.0 mm. Head large, rounded, a little longer than broad, with coarse longitudinal striations, the posterior margin straight, mandibles large; scape inserted close to the posterior margin of the clypeus, short, not reaching the back of the head; funicular segments

2-7, small, about as long as broad, segments 8-12 longer than broad, the last segment much larger than the others; thorax a little longer than the head, but not as wide; gaster small, about the size of the head. Length of head, 1.6 mm.; scape, 1.2 mm.; funiculus, 1.9 mm.; thorax, 1.8 mm.; gaster, 1.9 mm. Width of head, 1.3 mm.; thorax, 0.9 mm.; gaster, 1.2 mm.

Holotype.— No. 2922, M. C. Z. (S. H. Scudder).

Paratypes.— Nos. 2923-2925, M. C. Z.; no. 17,018a, University of Colorado.

Five other, rather poorly preserved specimens are in the Scudder collection. Even the holotype is not well preserved, but from a careful study of all the specimens at hand, I believe there is no question about the systematic position of the species.

AGROECOMYRMICINI, tribus nov.

LITHOMYRMEX, gen. nov.

Allied to *Agroecomyrmex* Wheeler (Baltic amber).

Female.— Head subquadrate; mandibles small; clypeus large; antennal scrobes present; antennae short, 12-segmented, with a two-jointed club; epinotum not armed; petiole and postpetiole short and compressed, the forewing with two cubital cells; head, thorax, and pedicel, coarsely sculptured.

Male.— Antennae 13-segmented; scape short, but a little longer than the second segment; sculpturing weaker than that of the female; forewing with two cubital cells.

Worker.— Very similar to the female, apparently differing only in the smaller size.

Genotype.— *Lithomyrmex rugosus*, sp. nov.

The two species placed in this genus are among the most unusual of the Florissant ants. The nearest relative of *Lithomyrmex* appears to be a Baltic amber genus, *Agroecomyrmex* Wheeler. The single specimen upon which Mayr originally based the species representing the latter genus was a poorly preserved worker, and he placed it in *Myrmica*. Fortunately, Professor Wheeler was able to examine three additional workers as well as a female and consequently to recognize its peculiar characteristics. *Lithomyrmex* is distinguished from *Agroecomyrmex* by the smaller mandibles and the large antennal club, but in other respects the two genera are very similar.

The tribe in which Wheeler placed *Agroecomyrmex* (1914), has subsequently been restricted so as to embrace only a fraction of the genera

originally included, so that a new tribe is established here to contain the amber genus and its Florissant relative. The tribe Agroecomymricini has several characters in common with three existing groups: the Cataulacini, Meranoplinae, and Cryptocerini. Its relationship with the first of these, which consist only of the Australian genus *Cataulacus*, is very slight, however, for the forewing in this genus lacks a discoidal cell and has only one cubital cell, and the antennae of the male and female are 11-segmented. In *Agroecomyrme* and *Lithomyrme* the wing has a discoidal cell and two cubital cells, the antennae of the female are 12-segmented and those of the male are 13-segmented. Of the Meranoplinae, the closest genus to *Agroecomyrme* is *Promeranoplus*, which is likewise confined to the Australian region. The female of this genus is still unknown, but the worker has 12-segmented antennae and the male, 13-segmented; the forewing of the male, like that of the females of the other known genera of the tribe, has a discoidal and a single cubital cell. In addition to these differences the thorax is quite unlike that of *Agroecomyrme*. The tribe Cryptocerini, which inhabits neotropical and southern nearctic regions, has the venation of the forewing like that of the Meranoplinae; the antennae of the male are 13-segmented, but those of the female are only 11-segmented. However, inasmuch as the 12-segmented condition of the antennae of the female in the Agroecomymricini is more primitive than that of 12 segments, I am inclined to believe that this latter tribe represents an earlier stage in the evolutionary process which produced the more highly specialized Cryptocerini.

LITHOMYRME RUGOSUS, sp. nov.

Plate 5, fig. 1, 3. Plate 8, fig. 2. Plate 11, fig. 3

Female.—Length, 8.0 mm. Head longer than broad, posterior and lateral margins straight; mandibles with a stout apical tooth, and a nearly smooth inner margin; scapes not reaching the posterior margin of the head, much broadened apically; funiculus also short, segments 3-9 about twice as broad as long, second segment about as broad as long, the last two segments forming a club, the last segment much larger than the penultimate; thorax a little longer than the head and about as wide; epinotum apparently unarmed; petiole with a small node; postpetiole shorter than the petiole, but higher; gaster small, about as long and broad as the thorax. Head, thorax, and petiole coarsely and reticulately rugose; the postpetiole and entire gaster with a series of coarse longitudinal striations; forewing with a closed dis-

coidal and two cubital cells. Length of head, 2.4 mm.; scape, 1.5 mm.; funiculus, 1.9 mm.; thorax, 2.2 mm.; gaster, 3.3 mm. Width of head, thorax and gaster, 1.8 mm.

Holotype.—No. 2926, M. C. Z. (S. H. Scudder).

Paratypes.—No. 2927a-b, 2931a-b, M. C. Z.; no. 17,019a, University of Colorado.

Male.—Head broader than long; eyes of moderate size; funicular segments about as broad as long, the last three segments somewhat larger than the others; postpetiole larger than the petiole; gaster small, nearly globular; head and thorax reticulately rugose, gaster smooth. Venation as in female. Length, 7.0 mm. Length of head, 0.9 mm.; scape, 1.0 mm.; funiculus, 2.4 mm.; thorax, 2.2 mm.; gaster, 2.7 mm.; forewing, 7.0 mm. Width of head, 1.5 mm.; thorax and gaster, 1.8 mm.

Allotype.—No. 2932, M. C. Z. (S. H. Scudder).

One of the striking features of this ant is the strong sculpturing on the gaster, the striations extending to the very end of the abdomen. As far as I am aware no other fossil or living species has the sculpturing extending that far posteriorly. This species is not a particularly rare one at Florissant; I have seen forty good specimens in the material at my disposal.

LITHOMYRMEX STRIATUS, sp. nov.

Plate 6, fig. 1

Female.—Length, 8.0 mm. Head nearly subtriangular; antennal scrobes well developed, probably more so than in *L. rugosus*; funicular segments 3-9 nearly as long as broad, the antennal club not so marked as in the previous species; thorax a little longer than the head and about as broad; postpetiole only a very little longer than the petiole; gaster about the size of the thorax; head rugosely striated, the postpetiole and the base of the gaster faintly striated, most of the gaster without sculpturing. Length of head, 1.9 mm.; scape, 1.0 mm.; funiculus, 1.4 mm.; thorax, 2.1 mm.; gaster, 2.1 mm.; forewing, 4.8 mm. Width of head, 1.3 mm.; thorax, 1.3 mm.; gaster, 1.8 mm.

Holotype.—No. 2933, M. C. Z. (S. H. Scudder).

Worker.—Length, 6.0 mm. Identical with the female except for size. Length of head, 1.8 mm.; thorax, 1.2 mm.; gaster, 3.0 mm.

Ergatotype.—No. 2934, M. C. Z. (S. H. Scudder).

Both castes of this species are represented by uniques, the female by a dorso-ventral specimen, and the worker by a lateral specimen. The worker is rather poorly preserved, but there can be no question as

to its systematic position. The species differs from the preceding in the smaller head, the longer funicular segments, the smaller postpetiole, and especially in the unsculptured gaster.

TRIBUS INCERTA

CEPHALOMYRMEX, gen. nov.

Female.— Robust; head exceedingly large, rounded; thorax short; gaster very small; antennae abbreviated, the funiculus apparently with only five or six segments; petiole pedunculate; postpetiole short but broad. (Venation unknown).

Genotype.— *C. rotundatus*, sp. nov.

CEPHALOMYRMEX ROTUNDATUS, sp. nov.

Plate 7, fig. 5. Plate 10, fig. 10

Female.— Length, 5.0 mm. Head nearly round, as broad as long; mandibles probably rather large; antennae unusually short, the scape less than one-half the length of the head; funiculus only a little longer than the scape; thorax about as long as the head, but not so broad; gaster much smaller than the head; forewing greatly exceeding the end of the abdomen. Length of head, 1.5 mm.; scape, 0.7 mm.; funiculus, 0.7 mm.; thorax, 1.5 mm.; gaster, 1.2 mm.; forewing, 6.0 mm. Width of head, 1.5 mm.; thorax, 1.2 mm.; gaster, 1.5 mm.

Holotype.— No. 2935, M. C. Z. (S. H. Scudder).

There are not enough details preserved in the single specimen which I have seen to determine definitely the affinities of this very strange ant. The head is proportionally larger than that of the female of any other ant known to me, and the unusually short antenna, together with its small number of segments, further isolates this species from any described forms. Until additional material showing the mandibles, eyes, and venation has been found, the relationship of this fossil must remain obscure.

DOLICHODERINAE

ANEURETINI

Of the many interesting ants in the Florissant shales, one of the most peculiar and certainly the least expected is a species belonging to the Aneuretini. At the present time this tribe contains one living genus, *Aneuretus* Emery, and two extinct genera in the Baltic amber, *Para-*

neuretus Wheeler and *Protaneuretus* Wheeler. Only two species of the living genus are known (*A. simoni* Emery and *A. butteli* Forel), both of which are confined to Ceylon. The significance of the amber genera was interpreted by Wheeler (1914) as follows: "The occurrence of the two genera *Paraneuretus* and *Protaneuretus* in the Baltic amber is of considerable interest on account of their close relationship to the living genus *Aneuretus*, which is regarded as a kind of connecting link between the subfamilies *Ponerinae* and *Dolichoderinae*. The amber species are in certain respects even more primitive and generalized and are of a larger size than the single known species of *Aneuretus*. They show that the tribe Aneuretini was long ago represented by several and peculiar genera, of which only one has survived the Tertiary." The discovery of this Florissant species, representing another genus close to *Paraneuretus*, supports the conclusion that the tribe was larger and more widely distributed during the Tertiary than it is at present.

MIANEURETUS, gen. nov.

Female.—Moderate size; head distinctly longer than broad, rounded, slightly narrowed anteriorly; sides convex; eyes large, ocelli present; mandibles triangular, with blunt teeth; antennae slender, with eleven subequal segments; thorax about as broad as the head; petiole much longer than broad, surmounted posteriorly by a small node; gaster of moderate size. (Venation unknown.)

Genotype.—*M. mirabilis*, sp. nov.

MIANEURETUS MIRABILIS, sp. nov.

Plate 3, fig. 5. Plate 10, fig. 1

Female (deälated).—Length, 9.0 mm. Head rather small, posterior margin straight, posterior angles broadly rounded; clypeus and front of head striated; mandibles small, with three large, bluntly rounded teeth on the inner margin; scapes not quite reaching the posterior margin of the head; funiculus moderately long, segments 3-11 somewhat longer than broad, 2 and 12 twice as long as broad; thorax about as broad as the head and a little longer; gaster about two and one-half times as long as the head, and twice as wide. Length of head, 1.6 mm.; scape, 1.4 mm.; funiculus, 2.0 mm.; thorax, 2.0 mm.; gaster, 4.2 mm. Width of head, 1.2 mm.; thorax, 1.2 mm.; gaster, 2.4 mm.

Holotype.—No. 2797, M. C. Z. (S. H. Scudder).

The single specimen of this species is so perfectly preserved that all

the details necessary for its proper classification are known. The gaster is the only part which shows much distortion, and this has been pressed so flat that the first segment is broken away from the second segment, producing much the appearance of a ponerine.

DOLICHODERINI

DOLICHODERUS (HYPOCLINEA) Lund

This genus has turned up regularly in the larger fossil ant deposits. Seven species have been recognized in the Baltic amber, two in the Radoboj beds, and three are described below from Florissant. This wide distribution in the Tertiary is only to be expected in view of the large area inhabited by the genus at the present time. It is interesting to observe, however, that although *Dolichoderus* is well represented in the eastern United States, no living species has been taken in the western part. The presence of these species in the Florissant shales shows that during the Miocene at least the genus extended much further westward than at the present time.

DOLICHODERUS ANTIQUUS, sp. nov.

Plate 4, fig. 6. Plate 9, fig. 1. Plate 10, fig. 2

Female.—Length, 6.5 mm. Moderately robust; head a little longer than broad, posterior margin only slightly concaved, posterior angles rounded, sides convex; mandibles large, with curved outer margins; scapes rather short, not quite reaching the posterior margin of the head; funicular segments 2–10 a little longer than broad, segments 1, 11 nearly twice as long as broad; eyes oval, of moderate size, situated at the middle of the sides of the head; thorax a little longer than the head and nearly as wide; epinotum concaved posteriorly, the dorsal part projecting over the petiole; scale of the petiole obtuse, nearly cuneiform; gaster about twice as long as the head, and about one and one-half times as broad; forewings short, with two cubital cells. The dorsal part of the head, epinotum and the sides of the rest of the thorax are marked with coarse rugose reticulations. Length of head, 1.5 mm.; scape, 1.0 mm.; funiculus, 1.5 mm.; thorax, 1.9 mm.; gaster, 3.1 mm.; forewing, 4.0 mm. Width of head, 1.2 mm.; thorax, 1.1 mm.; gaster, 1.9 mm.

Holotype.—No. 2798, M. C. Z. (S. H. Scudder).

Paratypes.—No. 10,000, Peabody Museum; no. 7824, Princeton Uni-

versity; no. (2), British Museum; no. 1700a, University of Colorado; no. 2, Wickham coll.; no. 22,973, A. M. N. H.

The holotype specimen is a dorsal view of the insect with the wings spread. The ocelli, although probably present in the species, are not visible because of the sculpturing on the head. The venation of the forewing is variable with respect to the shape of the discoidal cell and the point of divergence of the first intercubitus.

The worker of this species is represented, I believe, by two specimens of fair preservation. One of these is a lateral view of the thorax and gaster, and a dorsal view of the head; the other (ergatotype) is entirely a lateral specimen. No sculpturing is discernible but I infer that this is due to insufficient preservation. The head, thorax, and petiole are identical with those of the above female. The measurements of the ergatotype are as follows: length of specimen, 6.0 mm.; length of head, 1.3 mm.; thorax, 1.7 mm.; gaster, 3.0 mm. Width of head, 0.9 mm.

Ergatotype.— No. 2803, M. C. Z. (S. H. Scudder).

Paratype.— No. 10,002, Peabody Museum.

DOLICHODERUS ROHWERI, sp. nov.

Plate 4, fig. 1. Plate 9, fig. 7. Plate 10, fig. 3

Female.— Length, 5.3 mm. Moderately slender; head somewhat longer than broad, posterior margin only slightly concaved, posterior angles rounded; lateral margins curved; clypeus probably quite large; scape short, not reaching the posterior margin of the head; funicular segments 2-10 about as long as broad, the first and last somewhat longer; eyes oval, of moderate size, situated at the middle of the sides of the head; thorax about as broad as the head; epinotum only slightly concaved posteriorly, and not extending backward far enough to project over the petiole; scale of the petiole with its anterior face nearly vertical and the posterior face at about a 45-degree angle; gaster about two and one-half times the length of the head. Clypeus striated, the entire head and pronotum finely reticulate, the sculpturing on the epinotum coarser; posterior face of the scale of the petiole with a few longitudinal striations. Length of head, 1.2 mm.; scape, 0.6 mm.; funiculus, 0.9 mm.; thorax, 1.7 mm.; gaster, 2.4 mm. Width of head, 0.85 mm.

Holotype.— No. 2801, M. C. Z. (S. H. Scudder).

Paratypes.— No. 10,001, Peabody Museum; no. 2825, Princeton

University; no. 17,003a, University of Colorado; no. 22,974, A. M. N. H. no. (3), British Museum.

The holotype is a lateral view of the thorax and abdomen, but a dorsal view of the head. All the paratypes are lateral specimens. This female is readily distinguished from the preceding by its smaller size, finer sculpturing, structure of the epinotum and the longer petiole.

The worker of this ant appears to be represented by a single specimen, presenting a lateral view of the thorax and gaster; the head is bent under the thorax and is consequently rather obscure. There is no doubt, however, that this worker belongs to *Dolichoderus*, and since it is about the correct size and has sculpturing similar to that of the above female, it can be assigned to this species without much chance of error. The recognizable characters are as follows: length, 3.9 mm.; the last two or three funicular segments somewhat larger than the others; eyes nearly round, small; length of thorax, 1.8 mm.; meso-epinotal suture very distinct; posterior face of the epinotum more deeply concaved than in the female; length of gaster, 2.0 mm.

Ergatotype.— No. 2802a-b (S. H. Scudder).

TAPINOMINI

PROTAZTECA, gen. nov.

Allied to *Azteca*.

Female.— Head quadrate or subquadrate; mandibles large, triangular, with a distinct terminal tooth; anterior margin of clypeus straight; antennae 12-segmented, short, the scapes not reaching the posterior margin of the head, inserted close together near the clypeus; eyes oval, rather small, situated on the sides of the anterior half of the head; posterior face of the epinotum rounded; petiole rather small, gaster of moderate size; forewing with two closed cubital cells.

Male.— Only a little smaller than the female; head triangular; antennae 11-segmented; scape about as long as first funicular segments, as in *Azteca*; thorax and gaster relatively large; venation as in the female.

Worker.— Much smaller than the female, but otherwise similar to it.

Genotype.— *Protazteca elongata*, sp. nov.

Inasmuch as the extant genus *Azteca* is now confined to parts of South and Central America, the occurrence of this closely related genus in the Colorado Miocene is unusually interesting, especially since the female of *P. elongata* is one of the most numerous ants of the Florissant shales. *Azteca* and *Protazteca* are readily distinguished by several

characters: (1) the eyes in *Protazteca* are smaller and situated more posteriorly than in *Azteca*; (2) the scale of the petiole is more strongly inclined in *Azteca*; and (3) the forewings of *Protazteca* have two cubital cells, but those of *Azteca* have only one. This last distinction may be considered as indicative of the more primitive nature of the Miocene forms.

In 1906 Cockerell described a female ant from Florissant as *Ponera hendersoni*, which he placed in *Ponera* because of its similarity to the figure of *Ponera coarctata* Latr. in one of Wheeler's papers. His description of this ant is based almost entirely upon details of wing venation, so that it is impossible to recognize the species from the characters mentioned, and unfortunately the single specimen which Cockerell studied was lost shortly after the description was prepared. Wheeler subsequently pointed out (1910) that this ant could not be a true *Ponera* because of its large size. In 1927 Cockerell found three additional specimens (Sternberg collection, at the British Museum) which he believes to be this species, from a comparison with the same figure of *Ponera coarctata*. He placed the ant this time in *Euponera*, but did not designate any of these additional specimens as neotypes. Professor Cockerell kindly retained one of these newly acquired fossils so that I was able to examine it on my visit to Boulder in 1927. The specimen he showed me turned out to be a poorly preserved individual of the species which I am describing below as *Protazteca elongata*. At first I believed that the best procedure to clear up the difficulty would be to designate one of these new specimens of Cockerell's as the neotype of *Protazteca hendersoni* (= *Euponera hendersoni*). At that time my study of the Florissant ants was not completed, and after further examination of the material at hand I found two other species of *Protazteca*, both of which had as much and even more the appearance of *Ponera coarctata* (with which Cockerell made his original comparison) as *Protazteca elongata*. This accordingly brought up the question of the accuracy of Cockerell's determination of the specimens in the Sternberg collection, since twenty years had passed from the time of his description and the loss of the type, and especially since his description would apply to any one of three species of ants in the Florissant beds. In consideration of all the complications of the situation, it seems best to describe all three species of *Protazteca* as new, and to disregard the name *Euponera hendersoni*, until the type is found.

PROTAZTECA ELONGATA, sp. nov.

Plate 2, fig. 3. Plate 8, fig. 5. Plate 9, fig. 3. Plate 10, fig. 4

Female.—Length, 9.0 to 11.0 mm. Slender and elongate; head about twice as long as broad; posterior margin of head distinctly concaved, lateral margins straight and parallel; mandibles prominent, with a large terminal tooth and a number of irregular marginal teeth; posterior margin of clypeus prolonged backward at the middle; first three funicular segments twice as long as broad, the remaining segments about as long as broad; eyes elongate-oval; thorax about as long and as broad as the head; anterior face of the scale of the petiole slightly concaved, the posterior face convex; gaster slender, nearly twice as long as wide, and about twice as long as the head; forewing extending just a little beyond the end of the gaster. Length of head, 2.4 to 2.6 mm.; scape, 1.0 mm.; funiculus, 1.9 mm.; thorax, 2.7 to 3.0 mm.; gaster, 5.1 to 5.3 mm. Width of head and thorax, 1.3 to 1.5 mm.; gaster, 1.9 mm.

Holotype.—No. 2804a-b, M. C. Z. (S. H. Scudder).

Paratypes (♀).—Nos. 2805-2815, M. C. Z.; nos. 10,003-10,007, Peabody Museum; no. 7826, Princeton University; nos. 17,002, 17,003, University of Colorado; no. 78,791, U. S. N. M.; no. 22,978, A. M. N. H.; no. (4), British Museum; no. (1), Dublin Museum; nos. 8-15, Wickham collection; no. 13, Carnegie Museum.

The worker is much smaller than the female, but structurally similar, except that the head is not so elongate. Length, 5.0-7.0 mm. Length of head, 1.5 mm.; scape, 0.9 mm.; funiculus, 1.8 mm.; thorax, 2.1 mm.; gaster, 2.1 mm. Width of head, 0.9 mm.; thorax, 1.0 mm.; gaster, 1.8 mm.

Ergatotype.—No. 2816, M. C. Z. (S. H. Scudder).

Paratypes (♂).—No. 10,008, Peabody Museum; no. 22,979, A. M. N. H.; no. 78,791, U. S. N. M.

The male is a little smaller than the female, and moderately robust; head small, narrow, but quite long; eyes large, nearly round; scape short; the funicular segments a little longer than broad; thorax and abdomen stout; venation as in the queen. Length, 6.0 mm.; head, 1.5 mm.; scape, 0.5 mm.; funiculus, 1.3 mm.; thorax, 2.1 mm.; gaster, 3.0 mm.; forewing, 5.4 mm. Width of head, 7.0 mm.; thorax, 1.0 mm.; gaster, 1.8 mm.

Allotype (♀).—No. 2818, M. C. Z. (S. H. Scudder).

Paratypes.—Nos. 2819-2822, M. C. Z.; no. 10,009, Peabody Museum;

no. 17,001c, University of Colorado; no. 7827, Princeton University; no. 78,791, U. S. N. M.; no. 22,980, A. M. N. H.; no. (5), British Museum; no. (2), Dublin Museum; no. 16, Wickham collection; no. 14, Carnegie Museum.

As mentioned above, this species is one of the commonest of the Florissant ants. In the collections at my disposal I have found a total of about 800 females, 700 males, and 8 workers. With respect to this great abundance of individuals it is interesting to note that the males and females (probably also the neuters) are very variable in size. This variation is frequently so extreme that anyone who might compare isolated large and small females would readily consider the two as belonging to different species. Such, in fact, was my assumption when I began to study this species, but after several hundred specimens had been examined, I was able to recognize a complete series of specimens ranging in size from 9.0 to 11.0 mm. The holotype is one of the smaller specimens, but many of the paratypes are members of the larger end of the series.

The excessively slender head of the female of this species is indicative of the habits of the ant. A similarly elongate head occurs in recent species of several unrelated genera, i. e., *Azteca longiceps* Emery, *Pseudomyrma filiformis* Fab., and *Camponotus (Myrmostenus) mirabilis* Emery. Since all these ants live in hollow twigs, the exaggerated tenuity being an adaptation for this mode of life, we may reasonably assume that *P. elongata* had similar habits.

PROTAZTECA QUADRATA, sp. nov.

Plate 3, fig. 1. Plate 6, fig. 7. Plate 10, fig. 5

Female.—Length, 11.0 to 12.0 mm. Robust; head very large, about one and one-half times as long as broad; posterior margin of the head straight; lateral margins also straight and parallel; mandibles very large, with six sharp triangular teeth; the first two funicular segments at least twice as long as broad, the other segments about as long as broad; eyes situated a little anterior of the middle of the head; thorax narrower, and only a little longer than the head; scale of petiole low, truncate; gaster large, about twice as long and nearly twice as wide as the head. Length of head, 3.5 mm.; scape, 1.8 mm.; funiculus, 2.2 mm.; thorax, 3.6 mm.; gaster, 5.7 mm.; forewing, 7.0 mm. Width of head, 2.2 mm.; thorax, 1.8 mm.; gaster, 4.0 mm.

Holotype.—No. 2823a-b, M. C. Z. (S. H. Scudder).

Paratypes.—No. 2824, 2825, M. C. Z.; no. 10,010, Peabody Museum;

no. 7831, Princeton University; no. 17,002a, University of Colorado; no. 78,792, U. S. N. M.; nos. 22,962-63, A. M. N. H.; no. 17-19, Wickham collection; no. 15, Carnegie Museum.

The holotype specimen is one of the most perfectly preserved ants in the Florissant collection. The queen of this species can readily be distinguished from that of the preceding by the proportionally shorter and broader head, larger mandibles, and truncate scale of the petiole. The worker is represented by two specimens, one of which is nearly as splendidly preserved as the female. The head is about as large, comparatively, as that of the queen, but it is not as markedly quadrate, and the mandibles are less prominent. Measurements: length, 7.5 mm.; length of head, 2.1 mm.; scape, 1.2 mm.; funiculus, 1.8 mm.; thorax, 2.4 mm.; gaster, 3.6 mm. Width of head, 1.3 mm.; thorax, 1.0 mm.; gaster, 2.4 mm.

Ergatotype.—No. 2826, M. C. Z. (S. H. Scudder).

Paratype.—No. 10,011, Peabody Museum.

PROTAZTECA CAPITATA, sp. nov.

Plate 3, fig. 3. Plate 9, fig. 10

Female.—Length, 9.5 mm. Moderately robust; head very large, quadrate, posterior margin straight, posterior angles broadly rounded; mandibles of moderate size; all funicular segments a little longer than broad; eyes situated on the sides of the head, very near the middle line; thorax relatively slender, a little longer than the head, but not nearly as wide; gaster short, not quite twice as long or as wide as the head. Length of head, 2.4 mm.; scape, 1.3 mm.; funiculus, 1.9 mm.; thorax, 3.0 mm.; gaster, 4.5 mm. Width of head, 1.8 mm.; thorax, 1.4 mm.; gaster, 2.7 mm.

Holotype.—No. 2827a-b, M. C. Z. (S. H. Scudder).

Paratypes.—No. 10,012, Peabody Museum; no. 7832, Princeton Museum; no. 17,004a, University of Colorado; no. 78,793, U. S. N. M.; no. 22,961, A. M. N. H.; no. 20, Wickham collection; no. 16, Carnegie Museum.

There is a single obscure worker in the Scudder collection which I consider to belong to this species. The antennae, mandibles, and eyes are not preserved, but the shape of the head is so similar to that of the above female that I feel justified in this conclusion. The habitus of the worker can be seen in the photograph, and since no details of structure are preserved, I can only describe the insect by the following measure-

ments: length, 6.0 mm. Length of head, 1.5 mm.; thorax, 2.0 mm.; gaster, 2.1 mm. Width of head, 1.2 mm.; thorax, 0.4 mm.; gaster, 1.8 mm.

Ergatotype.— No. 2828, M. C. Z. (S. H. Scudder).

LIOMETOPUM Mayr.

The four living species which comprise this genus inhabit very disconnected regions. *L. apiculatum* Mayr occurs in Mexico, Arizona, New Mexico, and Colorado; *L. occidentale* Emery, in California and Oregon; *L. lindgreeni* Forel, in Burma and Assam; and *L. microcephalum* (Panzer), in southern Europe and Asia Minor. The Baltic amber contains one species, *L. oligocenicum* Wheeler, and the Radoboj beds another, *L. antiquum* Mayr. The two Florissant forms described below increase the number of extinct species to four, which equals that of those now living. The obvious conclusion is that the extant species are only a small remnant of a large series of forms which comprised the genus during the mid-Tertiary.

LIOMETOPUM MIOCENICUM, sp. nov.

Plate 3, fig. 6. Plate 8, fig. 3. Plate 9, fig. 8. Plate 10, fig. 8.

Plate 11, fig. 7

Female.— Length, 12.0 to 13.0 mm. Robust; head triangular, a little longer than its greatest width, posterior margin straight, lateral margins curved; mandibles large, triangular, with six or seven irregular teeth; scapes very short, not reaching the posterior margin of the head; first three funicular segments a little longer than broad, the remaining segments about as long as broad; eyes oval, of moderate size; thorax a little longer than the head, and nearly as broad; scale of petiole narrow, its anterior face vertical, and its posterior face inclined at an angle of about 60 degrees; gaster large, about three times as long as the head, and about twice as wide. Length of head, 3.8 mm.; scape, 2.0 mm.; funiculus, 3.5 mm.; thorax, 5.0 mm.; gaster, 10.5 mm.; forewing, 9.0 mm. Width of head, 3.3 mm.; thorax, 3.5 mm.; gaster, 7.0 mm.

Holotype.— No. 2829, M. C. Z. (H. F. Wickham).

Paratypes.— Nos. 2830–2840, M. C. Z.; nos. 10,013–10,015, Peabody Museum; nos. 7833–7837, Princeton University; no. 17,005a, b, c, University of Colorado; no. 78,794, U. S. N. M.; nos. 22,954–55, A. M. N. H.; no. (7–8), British Museum; no. (3–4), Dublin Museum; nos. 21–28, Wickham collection; no. 17, Carnegie Museum.

By far the majority of the females have the head flattened so that it is more nearly round than triangular, but the best specimens (i.e., those showing the least amount of distortion) have the head triangular, as shown in the drawing.

Male.—Somewhat smaller than the female; head very small in proportion to the rest of the insect; genitalia large, as in the members of this genus. Length, 9.5 mm. Length of head, 1.5 mm.; antennae, 2.4 mm.; thorax, 2.6 mm.; gaster, 4.9 mm.; forewing, 8.0 mm. Width of head, 1.2 mm.; thorax, 1.8 mm.; gaster, 3.0 mm.

Allotype (♂).—No. 2840, M. C. Z. (H. F. Wickham).

Paratypes (♂).—Nos. 2841-2849, M. C. Z.; no. 10,016, Peabody Museum; no. 7828, Princeton University; no. 17,005d, University of Colorado; no. 78,794, U. S. N. M.; nos. 22,956-57, A. M. N. H.; no. (9), British Museum; no. (5), Dublin Museum; nos. 29-30, Wickham collection; no. 18, Carnegie Museum.

Worker.—Much smaller than female; head a little longer than broad, more or less cordate; scape short; thorax not quite so long or so wide as the head; gaster about twice as long and one and one-half times as wide as the head. Length, 6.0 mm. Length of head, 2.7 mm.; thorax, 2.4 mm.; gaster, 5.8 mm. Width of head, 2.2 mm.; thorax, 1.3 mm.; gaster, 3.0 mm.

Ergatotype.—No. 2850, M. C. Z. (S. H. Scudder).

Although I have seen a number of other workers apparently belonging to this species, I have not designated them as paratypes, since none of them show the details which are necessary for satisfactory determination. This species stands a close second to *Protazteca elongata* as regards abundance.

LIOMETOPUM SCUDDERI, sp. nov.

Plate 4, fig. 4. Plate 9, fig. 4

Female.—Length, 8.0 mm. Robust; head triangular, a little longer than broad; posterior margin and angles rounded, lateral margins only slightly curved; mandibles of moderate size, with three or four prominent teeth; anterior margin of clypeus straight, posterior margin prolonged behind even more than in *L. miocenicum*; scapes not quite reaching the posterior margin of the head; funicular segments about as long as broad; eyes small, oval; thorax about one and one-half times as long, and about as wide as the head; gaster about three times as long as the head, and a little more than twice as wide; forewing short, not reaching the end of the gaster. Length of head, 1.5 mm.; scape, 0.9

mm.; funiculus, 1.5 mm.; thorax, 2.0 mm.; gaster, 5.0 mm.; forewing, 5.1 mm. Width of head, 1.4 mm.; thorax, 1.4 mm.; gaster, 2.4 mm.

Holotype.—No. 2851, M. C. Z. (S. H. Scudder).

Paratypes (♀).—Nos. 2852–2854, M. C. Z.; no. 10,017, Peabody Museum; no. 17,006a, University of Colorado; no. 78,795, U. S. N. M.; no. 22,959, A. M. N. H.; no. 2, Carnegie Museum.

The worker of this species appears to be represented by a few, rather poorly preserved individuals. Although none of them show details of structure, they have a habitus much like that of the worker of the preceding species but are smaller. Length, 5.0 mm. Length of head, 1.2 mm.; scape, 0.9 mm.; funiculus, 1.5 mm.; thorax, 1.5 mm.; gaster, 2.4 mm. Width of head and thorax, 0.9 mm.; gaster, 1.8 mm.

Ergatotype.—No. 2855, M. C. Z. (S. H. Scudder).

The female of this species is very similar to that of *L. miocenicum*, but can be distinguished from it by its smaller size and proportionally longer scapes.

ELAEOMYRMEX, gen. nov.

Female.—Head much longer than broad, narrowed anteriorly, posterior margin straight or slightly rounded, posterior angles broadly rounded, lateral margins nearly straight; mandibles prominent, triangular, with a large terminal tooth and five or six smaller teeth on the inner margin; clypeus large, anterior margin apparently straight, posterior margin with a prominent, median prolongation; entire clypeus with a series of fine striations which converge anteriorly; scapes of moderate size, not quite reaching the anterior margin of the head; eyes oval, of moderate size, situated at about the middle of the sides of the head; ocelli well developed; thorax rather long, slender; petiole small, the scale flattened, highest anteriorly; gaster slender; forewing with two closed cubital cells. The whole insect has a peculiar greasy appearance, unlike that of any other of the Florissant ants.

Worker.—Much smaller than the female but essentially the same in structure, except for somewhat smaller eyes. Clypeus striated as in the female.

Genotype.—*Elaeomyrmex gracilis*, sp. nov.

This genus has rather obscure affinities, but it probably belongs to Tapinomini, not very remote from *Iridomyrmex*.

ELAEOMYRMEX GRACILIS, sp. nov.

Plate 3, fig. 7. Plate 6, fig. 2. Plate 11, fig. 1

Female.—Length, 9.0 to 10.0 mm. Moderately slender; head rather long, oval, about one and one-half times as long as broad, posterior

margin rounded; first two and last funicular segments nearly twice as long as broad, the others only a little longer than broad; thorax not quite one and one-half times as long as the head, and about as wide as the head; scale of the petiole with several coarse, longitudinal corrugations at the base of the posterior face; gaster more than twice as long as the head, but not quite twice as wide; forewing short, not reaching the end of the gaster. Length of head, 2.1 mm.; scape, 1.5 mm.; funiculus, 2.3 mm.; thorax, 2.7 mm.; gaster, 4.2-4.8 mm.; forewing, 6.0 mm. Width of head, 1.7 mm.; thorax, 1.4 mm.; gaster, 2.4 mm.

Holotype.—No. 2863, M. C. Z. (S. H. Scudder).

Paratypes (♀).—Nos. 2864-2865, M. C. Z.; no. 10,021, Peabody Museum; no. 17,009a, University of Colorado; no. 78,797, U. S. N. M.

Worker.—For specific characters the measurements only can be given, but these, in addition to the description under the genus, will suffice to identify this caste. Length, 7.0 mm. Length of head, 1.8 mm.; scape, 1.2 mm.; funiculus, 1.8 mm.; thorax, 2.1 mm.; gaster, 2.9 mm. Width of head, 1.3 mm.; thorax, 1.2 mm.; gaster, 2.4 mm.

Ergatotype.—No. 2866, M. C. Z. (H. F. Wickham).

Paratypes (♀).—No. 10,021, Peabody Museum; no. 17,009b, University of Colorado; no. 22,969, A. M. N. H.

Both queens and workers of this species are fairly common in the Florissant shales. Including the types mentioned above, I have seen forty-two females and eight workers.

ELAEOMYRMEX COLORADENSIS, sp. nov.

Plate 3, fig. 2. Plate 9, fig. 2

Female.—Length, 8.0 mm. Moderately slender; head only a little longer than broad, with less rounded posterior angles than in the preceding species; mandibles of moderate size; scapes very nearly reaching the posterior margin of the head; the first two funicular segments, as well as the last, about twice as long as broad, the other segments very nearly as broad as long; thorax twice as long and about as wide as the head; petiole of moderate size, apparently without corrugations; gaster large, not quite three times as long as the head, its greatest width twice that of the head; forewing short, just reaching the end of the gaster. Length of head, 1.5 mm.; scape, 1.2 mm.; funiculus, 1.8 mm.; thorax, 2.7 mm.; gaster, 4.0 mm.; forewing, 6.0 mm. Width of head, 1.3 mm.; thorax, 1.3 mm.; gaster, 2.4 mm.

Holotype.—No. 2867, M. C. Z. (F. M. Carpenter).

Paratypes (♀).—No. 2868, 2869, M. C. Z.; no. 10,022, Peabody

Museum; no. 17,010a, University of Colorado; no. 78,798, U. S. N. M.; no. 6, Carnegie Museum.

The worker of this species appears to be represented by three specimens, which show no characters besides those given under the genus. Length, 6.0 mm. Length of head, 1.5; scape, 1.2; funiculus, 1.7 mm.; thorax, 2.1 mm.; gaster, 2.7 mm. Width of head, 1.0 mm.; thorax, 0.9 mm.; gaster, 1.8 mm.

Ergatotype.— No. 2870, M. C. Z. (S. H. Scudder).

Paratypes (♀).— No. 2871, M. C. Z.; no. 10,023, Peabody Museum.

The female of this species, which is very close to *E. gracilis* but much less common (29 specimens), can be distinguished from that of the latter by its shorter head, relatively longer thorax, and probably also by the lack of corrugations on the scale of the petiole. The worker can be separated from that of the preceding species only with considerable difficulty, but its head is also a little shorter.

IRIDOMYRMEX MAYR

This genus is now widely distributed over the tropical and subtropical regions of the world, reaching its maximum development in Australia. Only one species, *I. analis* E. Andre, is native to North America. As one would naturally expect from the primitive distribution of recent species, the genus is well represented in Tertiary deposits, five species having been found in the Baltic amber, and the two following in the Florissant beds. Our lack of knowledge of the details of the mandibles and clypeus of the Florissant species might seem to throw some doubt on their generic position, but both are obviously dolichoderines with affinities closer to *Iridomyrmex* than any other genus.

IRIDOMYRMEX FLORISSANTIUS, sp. nov.

Plate 2, fig. 4. Plate 10, fig. 7

Female.— Length, 6.0 mm. Moderately robust; head about one and one-half times as long as broad; posterior margin slightly curved, posterior angles broadly rounded, lateral margins slightly convex; mandibles small; scape reaching the posterior margin of the head; first funicular segment about twice as long as broad, the other segments as broad as long; thorax a little longer than the head and about as wide; epinotum rounded; petiole small, the scale inclined slightly forward; gaster about two and one-half times as long as the head, and twice as

wide; forewing with two cubital cells. Length of head, 1.2 mm.; scape, 0.7 mm.; funiculus, 0.9 mm.; thorax, 1.5 mm.; gaster, 3.0 mm. Width of head, 0.9 mm.; thorax, 0.9 mm.; gaster, 1.8 mm.

Holotype.—No. 2872, M. C. Z. (S. H. Scudder).

Paratypes (♀).—Nos. 2873–2875, M. C. Z.; no. 10,024, Peabody Museum; no. 17,011a, University of Colorado; no. 22,965, A. M. N. H.; no. 7, Carnegie Museum.

This female is not at all rare; I have seen 34 specimens. The worker is probably present among the several which I have not been able to determine.

IRIDOMYRMEX OBSCURANS, sp. nov.

Female.—Length, 8.0–9.0 mm. Moderately robust; head a little longer than broad, posterior margin quite straight, lateral margins distinctly curved; mandibles prominent; scape reaching the posterior margin of the head; first funicular segment about twice as long as broad, the others as broad as long; eye small; thorax a little longer than the head and about as wide; gaster of moderate size, a little more than twice as long as the head, and one and one-half times as broad; forewings with two cubital cells.

Holotype.—No. 78,799, U. S. N. M. (Lacoe collection).

This species is one of the most obscure of the Florissant ants, since nothing but the more general features are known. I have described it because the presence of 26 specimens in the material before me shows that it is fairly common in the deposit. Its habitus is so similar to that of the previous species that a figure seems unnecessary. It may be distinguished from *I. florissantius* by its larger size and more robust mandibles.

MIOMYRMICINI, tribus nov.

MIOMYRMEX, gen. nov.

Female.—Head of moderate size, longer than broad; posterior and lateral margins quite straight, sides nearly parallel; mandibles prominent, deeply corrugated, with four or five blunt teeth on the inner margin; anterior margin of clypeus prolonged, but abruptly truncate; posterior margin slightly prolonged backward; eyes large, situated rather high up on the sides, at about the middle line of the head; ocelli small, close together; antennae inserted close to the clypeus, exceedingly short, 12-segmented, the scapes not over one-half the length of the head, the funiculus only a little longer than the scape; epinotum

prolonged backward slightly over the petiole; scale of petiole large, more or less erect, nearly cuneiform; forewing with a closed cubital cell and a discoidal cell.

Male.— Nearly as large as the female; head small, triangular, about as broad as long; eyes very large, projecting, situated in the posterior half of the head; ocelli large, close together; mandibles small, narrow; antennae very short, composed of thirteen segments, the scape about as long as the first three segments; venation as in the female.

Worker.— Smaller than the female; head large, oval; eyes small; mandibles prominent; antennae like those of the female but with a thicker funiculus.

Genotype.— *Formica impactus* Ckll.

The affinities of *Miomymex* are rather obscure. In his original description Cockerell placed the genotype species in the Formicinae, as a true *Formica*, apparently because the venation of this form (one closed cubital cell and a discoidal) was similar to that of *Formica*. This type of venation, however, is not only found in other genera of Formicines, but also in many dolichoderines, including *Azteca* and *Iridomyrmex*. The venation, at any rate, is the only character which *Miomymex* and *Formica* have in common. The habitus of this peculiar extinct genus is much more suggestive of a dolichoderine than a formicine, and although it would be necessary to determine the nature of the cloacal opening in order to settle the matter, we may safely consider that *Miomymex* belongs to the former subfamily. There is, however, no known genus of the Dolichoderinae with such abbreviated antennae, and for this reason *Miomymex* requires a new tribe.

MIOMYRMEX IMPACTUS (Ckll.)

Plate 2, fig. 7. Plate 7, fig. 1, 2. Plate 10, fig. 6, 11

Formica impactus, Cockerell, T. D. A., 1927. Ann. Mag. Nat. Hist. (9), 19, p. 165.

Female.— Length, 16-17 mm. Robust; head rather long, subquadrate; mandibles with five blunt teeth; clypeus and anterior half of the head with a series of fine parallel striations; scapes slender and abbreviated, not reaching the posterior margin of the eyes; funicular segments nearly as broad as long, the terminal joints slightly larger than the rest; ocelli very close together; thorax a little longer than the head and about as broad; scale of the petiole with the anterior face vertical, posterior face inclined and slightly convex; gaster about two and one-half times as long as the head, and about twice as wide; fore-

wing short, not reaching the end of the gaster. Length of head, 3.3 mm.; scape, 1.2 mm.; funiculus, 1.5 mm.; thorax, 4.2 mm.; gaster, 8.5 mm.; forewing, 11.0 mm. Width of head, 2.4 mm.; thorax, 2.7 mm.; gaster, 4.5 mm.

Holotype.— At British Museum.

Homotypes.— Nos. 2856-58, M. C. Z.; no. 10,018, Peabody Museum; no. 7840, 7841, Princeton University; no. 17,007a, University of Colorado; no. 98,796, U. S. N. M.; no. 34, Wickham collection; no. 3, Carnegie Museum; no. 22,972, A. M. N. H.

Cockerell's description of this female, based upon a single specimen in the Sternberg collection, consists mainly of minute venational details, which, as I have shown above, are entirely useless for determination. He also assigned the following structural characters: "Length nearly 17 mm., anterior wing about 11 mm. Robust, dark brown, the abdomen sutures broadly hyaline; head rather regularly oval, not broadened behind; mandibles massive, minutely denticulate; lower margin of clypeus entire, gently arched; wings hyaline, with dark brown stigma and brown veins." As shown above the color of the Florissant ants cannot be used for specific determination, since it varies for the individual, and the hyaline nature of the abdominal sutures as well as the brown color of the veins and stigma are characters which apply to nearly every Florissant ant. Not being able to recognize the species from Cockerell's description, I examined his type just before it was sent to the British Museum with the rest of the Sternberg collection. My above description is based upon this type, as well as 37 additional specimens in the various collections loaned to me. It should be observed that I described the mandibles as having five blunt teeth, although Cockerell stated that they were "minutely denticulate." I was unable to find any mandibular teeth on the type specimen and believe that Cockerell mistook for teeth the irregularities of the somewhat fractured mandibles. A number of specimens collected by Scudder show these blunt teeth very clearly.

The male is represented by a single specimen showing merely the general characters and since it has been discussed under the genus, only the dimensions can be added. Length, 13.5 mm.; length of head, 2.1 mm.; antennae, 2.5 mm.; thorax, 4.2 mm.; gaster, 7.2 mm.; forewing, 8.0 mm. Width of head, 2.1 mm.; thorax, 4.2 mm.

Allotype.— No. 2859a-b, M. C. Z. (S. H. Scudder).

The worker is represented by a single specimen collected by Scudder, but is so much smaller in size than the above female that it might possibly belong to the next species. The head has more rounded pos-

terior angles, and convex sides; the eyes are elongate, situated on the sides of the head, at about the middle line; the antenna is as relatively short as that of the female, but has a much heavier funiculus. Length, 7.5 mm.; length of head, 2.4 mm.; scape, 0.4 mm.; funiculus, 0.5 mm.; thorax, 2.4 mm.; gaster, 3.0 mm. Width of head, 1.8 mm.; thorax, 1.2 mm.; gaster, 1.8 mm.

Ergatotype.— No. 2860, M. C. Z. (S. H. Scudder).

The female of *M. impactus* (Ckll.) is the largest of any of the Florissant ants. This feature, together with the striated head and especially the short antennae, makes the species readily recognizable.

MIOMYRMEX STRIATUS, sp. nov.

Plate 8, fig. 6. Plate 10, fig. 9

Female.— Length, 10.5 mm. Moderately robust; head much longer than broad, subquadrate, mandibles prominent, with four blunt teeth and deep corrugations; clypeus and frons finely striated; scapes very short, reaching to about the middle of the eyes; thorax about as long as the head and about as wide; gaster about two and one-half times as long as the head, and about twice as wide; forewing short; venation identical with that of the preceding species. Length of head, 2.3 mm.; scape, 0.6 mm.; funiculus, 0.9 mm.; thorax, 2.4 mm.; gaster, 6.0 mm.; forewing, 7.0 mm. Width of head, 1.7 mm.; thorax, 1.6 mm.; gaster, 3.0 mm.

Holotype.— No. 2861a-b, M. C. Z. (S. H. Scudder).

Paratype.— No. 2944a-b, M. C. Z.

The types are the only specimens of the female which I have been able to find. Fortunately these are very well preserved in most respects, and appear to be nearly identical with the foregoing species, except that they are only one-half as large. The main structural difference is the possession of four mandibular teeth, instead of five, as in *M. impactus*.

Male.— Length, 9.0 mm. Scape a little longer than the first two funicular segments, which are a little longer than broad; front of head with faint longitudinal striations, posterior part of head with similar striations arranged obliquely; thorax nearly two and one-half times as long as the head and much broader; gaster about three and one-half times as long as the head, and twice as wide; forewing exceeding the end of the abdomen. Length of head, 1.5 mm.; antennae, 1.8 mm.; thorax, 3.6 mm.; gaster, 4.8 mm.; forewing, 6.0 mm. Width of head, 1.5 mm.; thorax, 2.1 mm.; gaster, 2.7 mm.

Allotype.— No. 2862, M. C. Z. (H. F. Wickham).

Paratypes (♂).— Nos. 2945-6 M. C. Z.; no. 10,019, Peabody Museum; no. 17,008a, University of Colorado; no. 4, Carnegie Museum.

TRIBUS INCERTA

PETRAEOMYRMEX, gen. nov.

Female.— Small; head subquadrate; scapes short, thick; eyes small, situated on the sides of the head, anterior to the middle line; petiole very small; forewing with two cubital cells.

Genotype.— *P. minimus*, sp. nov.

The affinities of this genus are rather obscure, chiefly because of the lack of material showing the petiole. Additional fossils may indicate a close relationship to *Forelius*.

PETRAEOMYRMEX MINIMUS, sp. nov.

Plate 4, fig. 2

Female.— Length, 4.5 mm. Robust; head broad, only a little longer than wide, posterior margin concaved, posterior angles slightly rounded, lateral margins straight; scape not reaching the posterior margin of the head, funiculus also short; thorax a little longer than the head, about as wide; gaster nearly three times as long as the head, and about twice as wide. Length of head, 1.0 mm.; scape, 0.4 mm.; funiculus, 0.5 mm.; thorax, 1.3 mm.; gaster, 2.7 mm. Width of head, 0.9 mm.; thorax, 0.9 mm.; gaster, 1.8 mm.

Holotype.— No. 2943, M. C. Z. (S. H. Scudder).

Paratypes (♀).— No. 10,035, Peabody Museum; no. 17,021a, University of Colorado; no. 78,805, U. S. N. M.

This is the smallest Florissant female with two cubital cells in the forewing. It is not very common, there being only eleven specimens in the collections at hand.

FORMICINAE

FORMICINI

FORMICA Linné

This widely distributed genus is represented in the Tertiary by six Baltic amber species, several from the Radoboj formation, and three in the Florissant shales.

FORMICA ROBUSTA, sp. nov.

Plate 6, fig. 6. Plate 7, fig. 6

Female.—Length 9.0–10.0 mm. Robust; head triangular, about as long as broad, posterior margin straight, posterior angles rounded; mandibles quite large, with a prominent terminal tooth and a number of irregular smaller teeth; antennae slender, the scapes greatly exceeding the posterior margin of the head; eyes moderately large; thorax slender, nearly one and one-half times as long as the head, and a little broader; gaster about two and one-half times as long as the head, and twice as wide; forewing exceeding the end of the abdomen. Length of head, 1.5 mm.; scape, 1.5; funiculus, 2.2 mm.; thorax, 2.7 mm. gaster, 5.0 mm.; forewing, 7.8 mm. Width of head, 1.5 mm.; thorax, 1.8 mm.; gaster, 3.0 mm.

Holotype.—No. 2878, M. C. Z. (S. H. Scudder).

Paratype (♀).—Nos. 2879–2886, M. C. Z.; no. 10,025, Peabody Museum; no. 7842, Princeton University; no. 17,012a, Colorado University, no. 78,800, U. S. N. M.; no. 22,976, A. M. N. H.; no. 35, Wickham collection; no. 8, Carnegie Museum.

The heads of most of the females are much flattened and consequently more rounded than that of the holotype and some of the paratypes. The holotype specimen shows less distortion than any other, but the antennae and eyes are not preserved; these latter structures do appear in some of the paratypes (e.g., 2879). With very few exceptions the females are light brown, indicating that in all probability this was the original color of the insects. The female is the commonest of the formicines, some three hundred specimens having been recognized in the material at my disposal. A few of these fossils, which are otherwise identical with the above female, have a series of fine striations on the clypeus and part of the head. Since many living species of *Formica* (e.g., *F. truncicola*, and *F. rufa rufa*) have similar striations in the female and worker, it is very probable that all the queens of *F. robusta* would show these striations if they were sufficiently well preserved and in the proper position.

Male.—There are a number of males which appear to belong to this species. They are undoubtedly *Formica* and their size is consistent with that of the female, but as in the case of the males of most other species, only measurements can be given as specific characters. Length, 7.0 mm. Length of head, 1.2 mm.; scape, 1.5 mm.; funiculus, 2.7 mm.; thorax, 2.1 mm.; gaster, 3.6 mm.; forewing, 9.0 mm. Width of head, 1.2 mm.; thorax, 1.8 mm.; gaster, 2.1 mm.

Allotype.—No. 2887, M. C. Z. (S. H. Scudder).

Paratype (♂).—No. 2888, M. C. Z.

FORMICA COCKERELLI, sp. nov.

Plate 4, fig. 3

Female.—Length, 12.0 mm. Head nearly one and one-half times as long as broad, more or less triangular, posterior margin slightly rounded; mandibles small, teeth blunt; anterior margin of clypeus arched; antennae slender, the scapes greatly exceeding the posterior margin of the head; ocelli small, widely separated; thorax about one and one-half times as long and as broad as the head; gaster about two and one-half times as long as the head and twice as wide; head and thorax delicately striated. Length of head, 2.4 mm.; scape, 1.8 mm.; funiculus, 3.0 mm.; thorax, 3.6 mm.; gaster, 6.0 mm. Width of head, 1.8 mm.; thorax, 3.0 mm.; gaster, 3.6 mm.

Holotype.—No. 2889a-b, M. C. Z. (S. H. Scudder).

Paratypes (♀).—No. 78,806, U. S. N. M.

There are four males which I believe belong to this species: length, 9.0 mm. Length of head, 1.5 mm.; scape, 1.5 mm.; funiculus, 3.2 mm.; thorax, 3.0 mm.; gaster, 4.5 mm.; forewing, 9.0 mm. Width of head, 1.5 mm.; thorax, 10.8 mm.; gaster, 2.4 mm.

Allotype.—No. 2890, M. C. Z. (S. H. Scudder).

Paratypes (♂).—No. 10,026, Peabody Museum; no. 17,013a, University of Colorado.

This is not a common species, the types being the only specimens which I have seen. Both castes are readily distinguished from the preceding by their much larger size.

FORMICA GRANDIS, sp. nov.

Plate 6, fig. 3

Female.—Length, 13.0 mm. Head large, triangular, about one and one-half times as long as broad, posterior margin straight; mandibles rather small, with a long terminal tooth; antennae very long and slender, the scape nearly as long as the head; funicular segments about twice as long as broad; thorax relatively small, not over one and one-third times as long as the head, and about as wide; gaster small, not quite twice as long as the head; forewing extending beyond the end of the gaster. Length of head, 3.0 mm.; scape, 2.7 mm.; funiculus, 3.9 mm.; thorax, 4.0 mm.; gaster, 5.5 mm.; forewing, 10.8 mm. Width of head, 2.0 mm.; thorax, 2.3 mm.; gaster, 3.6 mm.

Holotype.—No. 78,801, U. S. N. M. (Lacoe collection.)

Paratype.—No. 2891, M. C. Z.

This species, which is also very rare, is distinguished from the preceding by its much larger size, and the longer antennae. It is the largest of the Formicinae of Florissant.

LASIUS Mayr

This holartic genus is already represented in the Tertiary of the Baltic amber and the Radoboj beds; the Florissant shales contain one common species.

LASIUS PERITULUS (Ckll.)

Plate 5, fig. 6. Plate 7, fig. 7

Tetramorium peritulum, Cockerell, T. D. A., 1927. Ann. Mag. Nat. Hist., (9), 19, p. 165.

Cockerell based this species on a fairly well-preserved male which I examined before it was sent to the British Museum. Since none of the characters given by Cockerell serve to identify the ant generically or specifically, and especially since it was not originally assigned to the proper subfamily, I have redescribed the species, mainly from the queen.

Female.—Length, 7.5–8.0 mm. Moderately robust; head triangular, small, about one and one-half times as long as its greatest width; posterior margin straight, posterior angles broadly rounded; mandibles of moderate size, with a long terminal tooth, and a number of irregular smaller teeth; antennae slender, scapes slightly exceeding the posterior margin of the head; funicular segments 2–5 about as broad as long, segments 6–12 longer than broad; eyes oval, rather small; thorax, oval, about one and one-half times as long as the head; petiole small, the node cuneiform; gaster relatively large, about three and one-half times as long as the head; forewing greatly exceeding the end of the gaster. Length of head, 1.3 mm.; scape, 0.9 mm.; funiculus, 1.3 mm.; thorax, 1.9 mm.; gaster, 4.8 mm.; forewing, 7.8 mm. Width of head, 0.9 mm.; thorax, 1.3 mm.; gaster, 4.8 mm.

Allotype (♀).—No. 2892, M. C. Z. (S. H. Scudder).

Paratypes (♀).—Nos. 2893–2895, M. C. Z.; no. 10,027, Peabody Museum; nos. 7843, 7844, Princeton University; no. 17,014a, b, University of Colorado; no. 78,802, U. S. N. M.; no. 22,982, A. M. N. H.; no. (10), British Museum; no. 9, Carnegie Museum.

Male.—Small, about one-half the size of the female; node of petiole small, cuneiform; gaster short, rounded. Length, 4.5 mm. Length of head, 0.9 mm.; scape, 0.4 mm.; funiculus, 1.2 mm.; thorax, 1.2 mm.;

gaster, 1.9 mm.; forewing, 4.3 mm. Width of head, 0.6 mm.; thorax, 0.9 mm.; gaster, 0.9 mm.

Holotype (♂).— In British Museum.

Just why Cockerell considered this male to belong to *Tetramorium* is not at all clear, for there is no possibility of its being even a myrmicine. Both castes are very abundant; I have seen over four hundred females and some thousand males, most of which are well preserved. The worker of such a common species must be present in the deposit also, but I have not been able to recognize it.

CAMPONOTINI

CAMPONOTUS Mayr

Inasmuch as this genus is cosmopolitan at the present time, its occurrence in the various Tertiary deposits is only to be expected. One species (*C. menzei* Mayr) has been found in the Baltic amber, one in the Gurnet Bay Oligocene (*C. brodei* Donisthorpe) and several in the Oeningen and Radoboj beds. Three species are represented in the Florissant shales.

CAMPONOTUS FUSCIPENNIS, sp. nov.

Plate 5, fig. 4. Plate 11, fig. 6

Female.—Length, 11.0 mm. Robust; head rounded, very large, nearly twice as long as broad, posterior margin straight, posterior angles slightly rounded, lateral margins convex; mandibles of moderate size, triangular, with a few small teeth; clypeus large; scapes not quite reaching the posterior margin of the head; eyes small, elongate, placed well back on the posterior half of the head; thorax about as long as the head, but not as wide; gaster about one and one-half times as long as the head, and nearly twice as broad; forewing reaching the tip of the gaster, and with a distinct brown patch around the pterostigma. Length of head, 3.0 mm.; scape, 1.5 mm.; funiculus, 2.1 mm.; thorax, 3.0 mm.; gaster, 4.8 mm.; forewing, 8.5 mm. Width of head, 1.8 mm.; thorax, 1.5 mm.; gaster, 3.0 mm.

Holotype.—No. 2897, M. C. Z. (F. M. Carpenter).

Paratypes (♀).—No. 10,029, Peabody Museum; no. 17,015a, University of Colorado.

This species, which is easily recognizable by the brown patch on the wing, is represented by only four specimens, so it is apparently very rare.

CAMPONOTUS MICROCEPHALUS, sp. nov.

Plate 6, fig. 4. Plate 11, fig. 8

Female.—Length, 8.0 mm. Moderately slender; head small, elongate, about twice as long as broad, posterior margin short, nearly straight; posterior angles broadly rounded, lateral margins convex; mandibles rather large in comparison with the size of the head; scapes not reaching the posterior margin of the head; funicular segments about as long as broad; thorax a little longer than the head, and nearly twice as wide; gaster about three times as long as the head, and nearly three times as wide; wing just reaching the tip of the abdomen. Length, of head, 1.3 mm.; scape, 1.0 mm.; funiculus, 1.5 mm.; thorax, 1.8 mm.; gaster, 4.2 mm.; forewing, 5.4 mm. Width of head, 7.0 mm.; thorax, 1.5 mm.; gaster, 2.5 mm.

Holotype.—No. 2898, M. C. Z. (S. H. Scudder).

This ant has been described from a rather poorly preserved individual, but the small head will enable easy recognition.

CAMPONOTUS PETRIFACTUS, sp. nov.

Plate 6, fig. 5

Worker.—Length, 10.0 mm. Head oval, nearly twice as long as broad, with a rounded posterior margin; mandibles triangular, slender, armed with three sharp teeth; antennae slender, inserted close to the middle line of the head, all the segments about twice as long as broad; eyes small, placed well back on the posterior half of the head; thorax slender, much longer than the head, but not nearly as broad. Length of head, 2.4 mm.; scape, 2.4 mm.; funiculus, 3.0 mm.; thorax, 4.0 mm.; gaster, 3.6 mm. Width of head, 1.8 mm.; thorax, 1.5 mm.; gaster, 3.0 mm.

Holotype.—No. 2936, M. C. Z. (S. H. Scudder).

Paratypes.—No. 10,034, Peabody Museum; no. 17,020a, University of Colorado; no. 22,964, A. M. N. H.

The large size of this worker, as well as the shape of the head, shows that it cannot be associated with either of the two preceding queens. Only seven specimens have been found.

V. COMPARISON OF THE TERTIARY AND RECENT ANTS
OF NORTH AMERICA

With the completion of our examination of the ants known from the Tertiary rocks of North America, we are in a position to compare this

fauna with that now occupying the same area. In doing this, however, it must be borne in mind that our knowledge of the Tertiary ants is very meagre, partly because the forms found at any one locality represent only the fauna which existed in a certain environment. For this reason the absence of a genus from a deposit only indicates that it was absent in that particular environment; it may very well have been present at the same time under different conditions, which did not favor preservation.

The recent ant fauna of North America has already been discussed by Wheeler in several publications (1908, 1910, 1917, 1928), so that only a brief survey need be presented here. Excluding a few types which are now restricted to the nearctic region (*Myrmecocystus*, *Veromessor*, *Novomessor*, etc.), and which probably had diverse origins, the North American genera may be conveniently separated into three groups, each with a definite tendency in geographical distribution:

1. The first of these contains the genera which are limited to the New World, and which are almost entirely confined to the neotropical region, only a few species extending as far northward as the southern part of the nearctic. Here belong *Eciton*, *Neoponera*, *Pachycondyla*, *Pogonomyrmex*, *Cryptocerus*, *Atta*, *Forelius*, etc.

2. The second division consists of genera which are widely distributed in the tropics of both hemispheres and which are represented in the temperate regions by a small number of species or subgenera, as *Stigmatomma*, *Sysphincta*, *Monomorium*, *Pheidole*, *Leptogenys*, etc.

3. The last group includes those genera which are cosmopolitan or which inhabit the holarctic regions, as *Ponera*, *Stenamma*, *Formica*, *Lasius*, *Camponotus*, etc.

None of the American Tertiary ants belong to genera which are now restricted to the nearctic region, just as none of the amber species can be referred to genera confined to the palearctic. On the other hand, the first group of genera defined above is well represented in the Florissant shales, by *Archiponera* (a close relative of *Dinoponera*), *Pseudomyrma*, *Pogonomyrmex*, and *Protazteca*. The second division is represented by *Pheidole*, *Dolichoderus*, and *Iridomyrmex*; and the third, by *Aphaenogaster*, *Liometopum*, *Formica*, *Lasius*, and *Camponotus*. It is obvious, therefore, that the ant fauna of North America contained the same geographical elements during the Tertiary as it does in recent times. The only genera (*Novomessor*, etc.) which now exist in this area, and which may have been excluded from the Tertiary fauna, probably arose during a later period than the Miocene. We cannot, of course, derive detailed conclusions from such a small amount of evidence without becoming

too speculative, but it is obvious that the North American ant fauna of the mid-Tertiary was as highly developed as that of Europe, for while the number of species, and consequently genera, is far less in the former than in the latter, the difference is due entirely to the Baltic amber, which happened to be an ideal medium for the preservation of the ants. The presence of four genera with neotropical affinities in the Florissant shales, and especially the fact that one of them (*Protazteca*) is the predominant genus of the fauna, is strongly suggestive that during the mid-Tertiary the nearctic ant fauna was rich in genera which are now restricted to the neotropical region.¹ The present limitation of the second group of genera mentioned above to the southern portion of the nearctic is probably the result of the cool climate which enveloped the northern region during the Pleistocene glaciation.

Although the tendency for some of the Florissant insects to show relationship to Old World forms (e.g. *Glossina*) has already been observed by Cockerell, it is worth while to consider the two genera of ants which show similar affinities — *Mianeuretus* and *Messor*. The presence of the former in these shales, and of *Protaneuretus* and *Paraneuretus* in the Baltic amber supports the conclusion derived from morphological studies of *Aneuretus* that the tribe Aneuretini is a primitive one, and shows that it was once widely distributed. The probable occurrence of *Messor* is also of much interest, since this genus is now confined to palearctic, Ethiopian, and northern Indian regions. The two nearctic genera, *Novomessor* and *Veromessor*, which are very closely related to *Messor*, may be descendents of a branch of the latter which existed in North America during the Tertiary. The presence of these Old World genera in the Colorado Miocene is analogous to that of the neotropical genus, *Erebomyrma*, in the Baltic amber.

Perhaps the most important contribution of the North American fossil ants is to our appreciation of the age of the family. For although our knowledge of the mid-Eocene ants (Green River) is very fragmentary, it is sufficient to prove that the fauna of the early Tertiary was not only large and varied, but essentially modern. The fact that ants are not common in the Green River formation is not necessarily an indication that they were rare at the time of the existence of the biota, but only that the conditions were not favorable for their preservation; the macerated condition of all the known ants of this deposit strongly suggests that their nests were remote from the lakes and that the insects were carried to the latter by streams or freshets. Not only

¹ Brues has observed (1910) that some of the parasitic Hymenoptera of Florissant also show neotropical affinities.

were these early Tertiary ants highly differentiated morphologically, but as Wheeler has shown (1914) the Lower Oligocene forms (Baltic amber) had a social life as highly developed as the recent species, some of the amber workers being even polymorphic (*Pseudolasius* and *Dimorphomyrmex*). "That many of them had learned to attend plant-lice and had therefore become 'trophobiotic' is shown by a block of amber in the Königsberg Coll. containing a number of workers of *Iridomyrmex goepperti*, together with a lot of their Aphid wards. That the amber ants kept myrmecophiles in their nests can scarcely be doubted, for at least three genera of Paussidae¹ (*Cerapterus*, *Pleuropterus* and an undescribed genus) are cited by Klebs in his list of amber Coleoptera. That these ants also had Acarine parasites is shown by two workers of *Lasius schiefferdeckeri* in the Königsberg Coll., each bearing a mite attached to the base of the hind tibiae. These specimens also show that the mites had already acquired the peculiar habit of affixing themselves to very definite regions of their host's integument." It is clear, therefore, from the specialized social habits of the Oligocene ants, and the high differentiation of those of the Eocene, that the family must have originated well back in the Mesozoic. While, of course, the Cretaceous period is almost a blank as far as any group of insects is concerned, it seems hardly possible that the Formicidae could have reached such a high state of development by the early Tertiary, if they had originated in the Cretaceous period, as suggested by Handlirsch (1908), or even in the Upper Jurassic, as proposed by Emery (1920). And although it may be difficult to imagine ants included within the same fauna as the gigantic Protodonata of the Permian, which Wheeler suggests as the possible time of their origin, the discovery of comparatively highly specialized Hymenoptera in the Jurassic of Turkestan (Martynov, 1925), leads us to believe that the ants were similarly developed during that period of the earth's history. Probably the chief reason why they have not already turned up in this formation is that the primitive groups, as the Dorylinae, Cerapachinae, and Ponerinae, are either subterranean or terricolous and consequently not likely to be entombed in a lake deposit. At any rate, the problem of the origin of the Formicidae, both in time and space, must wait for its solution until ants have been discovered in pre-Tertiary deposits.

¹ Wasmann (S. J.) has more recently described the amber Paussidae. (*Zool. Anzeiger*, **68** (1/2), p. 25-30, 1926.)

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EXPLANATION OF PLATES

PLATE 1

PLATE 1

Archiponera wheeleri, sp. nov., Florissant, Colorado. Obverse of holotype.
(♂). × 8. Note eyes, clypeus, mandibles, and abdominal constriction.



PLATE 2

- Fig. 1. *Archiponera wheeleri*, sp. nov., Florissant. Reverse of holotype. (♀).
× 4.5.
- Fig. 2. *Pseudocamponotus elkoanus*, sp. nov., Elko, Nevada. Holotype. (♀).
× 5.
- Fig. 3. *Protazteca elongata*, sp. nov., Florissant, Colorado. Obverse of holotype.
(♀). × 4.
- Fig. 4. *Iridomyrmex florissantius*, sp. nov., Florissant. Obverse of holotype.
(♀). × 6.
- Fig. 5. *Archimyrme rostratus* Ckll., Green River shales, Roan Mountain,
Colorado. Reverse of holotype. (♀). × 2.5.
- Fig. 6. *Eoformica pingue* (Scudder), Green River shales, White River, Utah.
Homotype no. 19. (♂). × 6.
- Fig. 7. *Miomyrme impactus* (Ckll.), Florissant, Colorado. Obverse of homo-
type no. 2857. (♀). × 3.



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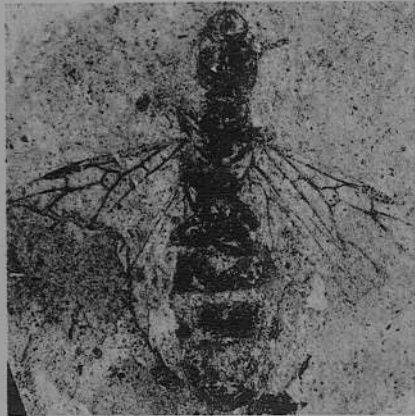
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PLATE 3

PLATE 3

- Fig. 1. *Protazteca quadrata*, sp. nov., Florissant. Obverse of holotype. (♀).
× 5.
- Fig. 2. *Elaeomyrmex coloradensis*, sp. nov., Florissant. Holotype. (♀). × 6.
- Fig. 3. *Protazteca capitata*, sp. nov., Florissant. Obverse of holotype. (♀).
× 3.5.
- Fig. 4. *Pseudomyrma extincta*, sp. nov., Florissant. Holotype. (♀). × 5.
- Fig. 5. *Mianeuretus mirabilis*, sp. nov., Florissant. Holotype. (♀). × 5.
- Fig. 6. *Liometopum miocenicum*, sp. nov., Florissant. Obverse of holotype.
(♀). × 3.5.
- Fig. 7. *Elaeomyrmex gracilis*, sp. nov., Florissant. Obverse of holotype. (♀).
× 4.



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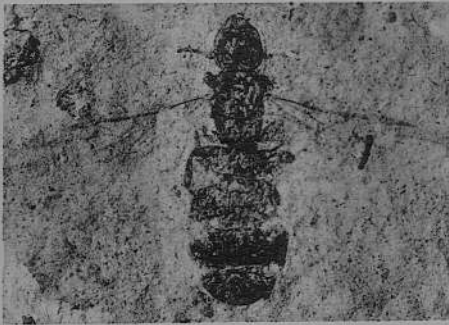
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PLATE 4

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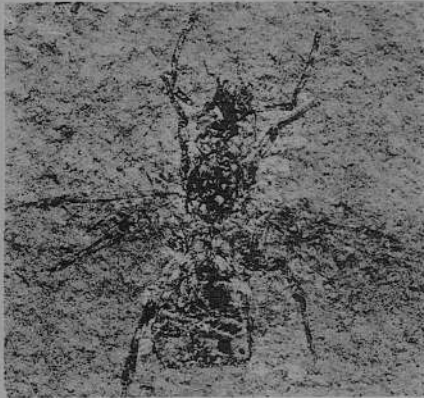
- Fig. 1. *Dolichoderus rohweri*, sp. nov., Florissant. Obverse of holotype. (♀).
× 9.
- Fig. 2. *Petraeomyrmex minimus*, sp. nov., Florissant. Obverse of holotype.
(♂). × 10.
- Fig. 3. *Formica cockerelli*, sp. nov., Florissant. Obverse of holotype. (♀).
× 3.
- Fig. 4. *Liometopum scudleri*, sp. nov., Florissant. Holotype. (♀). × 5.5.
- Fig. 5. *Messor sculpturatus*, sp. nov., Florissant. Holotypes. (♀). × 5.5.
- Fig. 6. *Dolichoderus antiquus*, sp. nov., Florissant. Obverse of holotype. (♀).
× 6.



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PLATE 5

PLATE 5

- Fig. 1. *Lithomyrmex rugosus*, sp. nov., Florissant. Paratype no. 17,019a. (♀).
× 5.5.
- Fig. 2. *Pheidole tertiaria*, sp. nov., Florissant. Holotype. (♀). × 7.
- Fig. 3. *Lithomyrmex rugosus*, sp. nov., Florissant. Obverse of holotype. (♀).
× 5.5.
- Fig. 4. *Camponotus fuscipennis*, sp. nov., Florissant. Holotype. (♀). × 6.
- Fig. 5. *Aphaenogaster mayri*, sp. nov., Florissant. Holotype. (♀). × 5.
- Fig. 6. *Lasius peritulus* (Ckll.), Florissant. Allotype. (♀). × 5.



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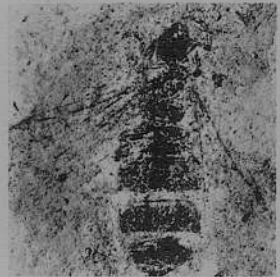
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PLATE 6

PLATE 6

- Fig. 1. *Lithomyrmex striatus*, sp. nov., Florissant. Holotype. (♀). × 7.
Fig. 2. *Elaeomyrmex gracilis*, sp. nov., Florissant. Ergatotype. × 6.
Fig. 3. *Formica grandis*, sp. nov., Florissant. Holotype. (♀). × 3.5.
Fig. 4. *Camponotus microcephalus*, sp. nov., Florissant. Holotype. (♀). × 5.
Fig. 5. *Camponotus petrifactus*, sp. nov., Florissant. Holotype. (♂). × 4.
Fig. 6. *Formica robusta*, sp. nov., Florissant. Holotype. (♀). × 4.
Fig. 7. *Protazteca quadrata*, sp. nov., Florissant. Ergatotype. × 4.5.



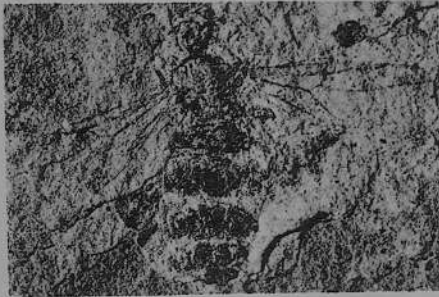
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PLATE 7

PLATE 7

- Fig. 1. *Miomymex impactus* (Ckll.), Florissant. Ergatotype. $\times 5$.
Fig. 2. *Miomymex impactus* (Ckll.), Florissant. Allotype. (σ). $\times 2.5$.
Fig. 3. *Aphaenogaster mayri*, sp. nov., Florissant. Allotype. (σ). $\times 8$.
Fig. 4. *Aphaenogaster donisthorpei*, sp. nov., Florissant. Holotype. (φ).
 $\times 7.5$.
Fig. 5. *Cephalomyrmex rotundatus*, sp. nov., Florissant. Holotype. (φ). $\times 8$.
Fig. 6. *Formica robusta*, sp. nov., Florissant. Allotype. (σ). $\times 5$.
Fig. 7. *Lasius peritulus* (Ckll.), Florissant. Specimen no. 2896. (σ). $\times 8$.



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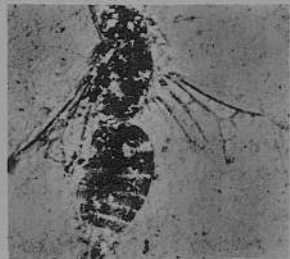
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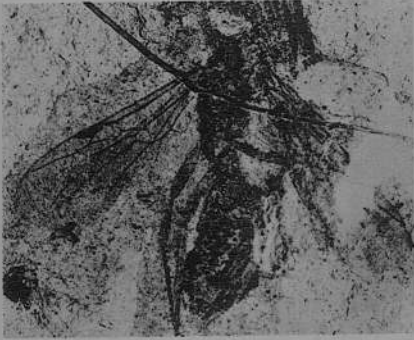


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PLATE 8

PLATE 8

- Fig. 1. *Archiponera wheeleri*, sp. nov., Florissant. Allotype. (♂). × 3.
Fig. 2. *Lithomyrmex rugosus*, sp. nov., Florissant. Allotype. (♂). × 5.
Fig. 3. *Liometopum miocenicum*, sp. nov., Florissant. Allotype. (♂). × 4.
Fig. 4. *Aphaenogaster mayri*, sp. nov., Florissant. Paratype no. 2912a. (♀).
× 8.5.
Fig. 5. *Protazteca elongata*, sp. nov., Florissant. Allotype. (♂). × 7.
Fig. 6. *Miomymex striatus*, sp. nov., Florissant. Allotype. (♂). × 5.



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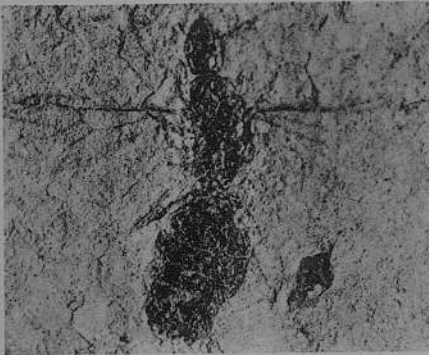
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PLATE 9

PLATE 9

- Fig. 1. *Dolichoderus antiquus*, sp. nov., Florissant. Ergatotype. × 10.
Fig. 2. *Elaeomyrmex coloradensis*, sp. nov., Florissant. Ergatotype. × 7.
Fig. 3. *Protazteca elongata*, sp. nov., Florissant. Ergatotype. × 7.
Fig. 4. *Liometopum scudderi*, sp. nov., Florissant. Ergatotype. × 10.
Fig. 5. *Aphaenogaster mayri*, sp. nov., Florissant. Ergatotype. × 7.
Fig. 6. *Pogonomyrmex fossilis*, sp. nov., Florissant. Holotype. (♀). × 7.
Fig. 7. *Dolichoderus rohweri*, sp. nov., Florissant. Ergatotype. × 10.
Fig. 8. *Liometopum miocenicum*, sp. nov., Florissant. Ergatotype. × 6.
Fig. 9. *Lithomyrmex striatus*, sp. nov., Florissant. Ergatotype. × 6.
Fig. 10. *Protazteca capitata*, sp. nov., Florissant. Ergatotype. × 6.



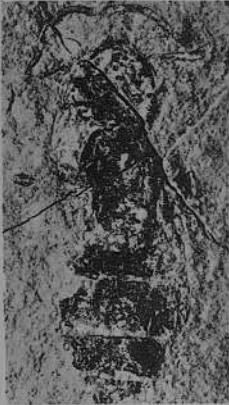
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PLATE 10

PLATE 10

- Fig. 1. *Mianeuretus mirabilis*, sp. nov. ♀.
Fig. 2. *Dolichoderus antiquus*, sp. nov. ♀.
Fig. 3. *Dolichoderus rohweri*, sp. nov. ♀.
Fig. 4. *Protazteca elongata*, sp. nov. ♀.
Fig. 5. *Protazteca quadrata*, sp. nov. ♀.
Fig. 6. *Miomymex impactus* (Ckll.). ♀.
Fig. 7. *Iridomyrmex florissantius*, sp. nov. ♀.
Fig. 8. *Liometopum miocenicum*, sp. nov. Head. ♂.
Fig. 9. *Miomymex striatus*, sp. nov. Head. ♂.
Fig. 10. *Cephalomyrmex rotundatus*, sp. nov. ♀.
Fig. 11. *Miomymex impactus* (Ckll.). ♀.

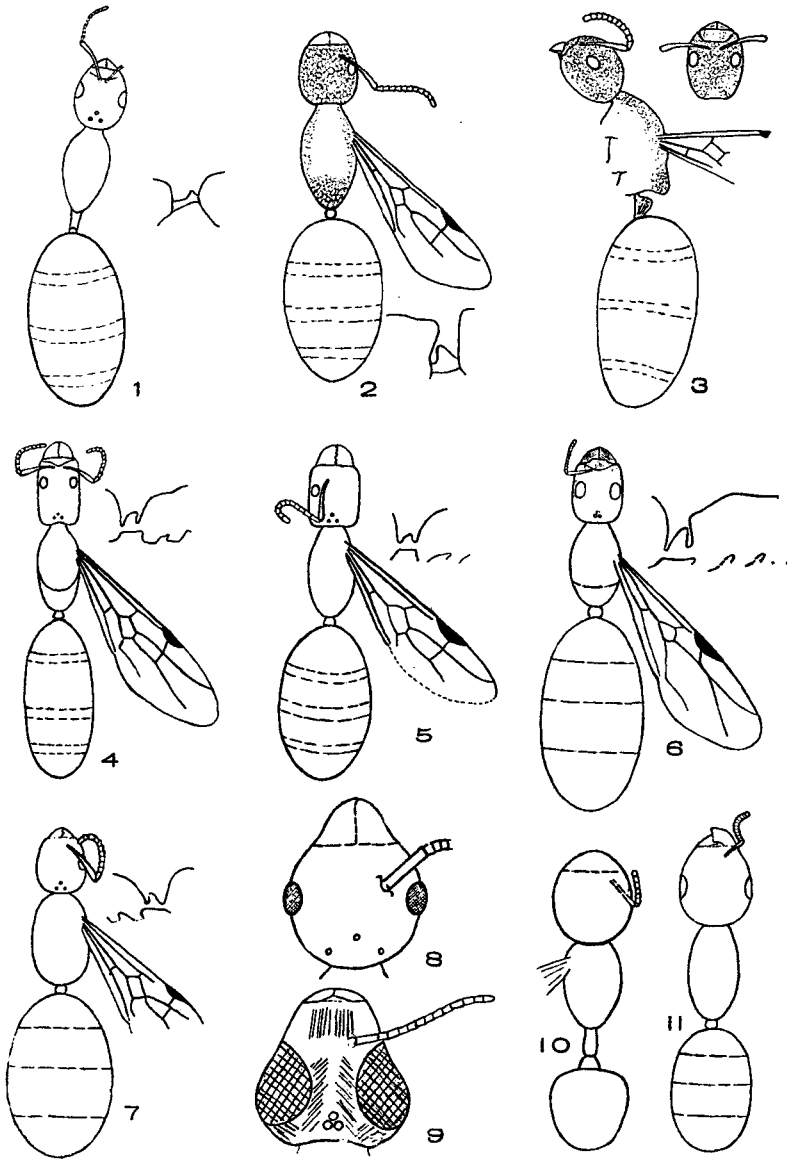


PLATE 11

PLATE 11

- Fig. 1. *Elaeomyrmex gracilis*, sp. nov. ♀.
Fig. 2. *Pheidole tertiaria*, sp. nov. ♀.
Fig. 3. *Lithomyrmex rugosus*, sp. nov. ♀.
Fig. 4. *Aphaenogaster mayri*, sp. nov. ♀.
Fig. 5. *Messor sculpturatus*, sp. nov. ♀.
Fig. 6. *Camponotus fuscipennis*, sp. nov. ♀.
Fig. 7. *Liometopum miocenicum*, sp. nov. ♀.
Fig. 8. *Camponotus microcephalus*, sp. nov. ♀.
Fig. 9. *Lasius peritulus* (Ckll.). ♀.

